

# POSTCANINE OCCLUSION IN CYNODONTS AND TRITYLODONTIDS



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# POSTCANINE OCCLUSION IN CYNODONTS AND TRITYLODONTIDS

By A. W. CROMPTON

## CONTENTS

I. INTRODUCTION . . . . .	30
II. POSTCANINE DENTITION OF THE PROCYNOSUCHIDAE AND GALESAURIDAE . . . . .	32
III. POSTCANINE DENTITION OF THE DIADEMODONTIDAE AND TRIRACHODONTIDAE . . . . .	35
IV. POSTCANINE DENTITION OF THE TRAVERSODONTIDAE . . . . .	40
1. Description of three new species of <i>Scalenodon</i> . . . . .	41
2. Occlusion and jaw movements in <i>Scalenodon angustifrons</i> . . . . .	44
3. Occlusion and jaw movements in <i>Scalenodon hirschsoni</i> . . . . .	49
4. Postcanine dentition of <i>Scalenodon attridgei</i> . . . . .	53
5. Postcanine dentition of <i>Scalenodon charigi</i> . . . . .	54
6. Occlusion and jaw movements in a species of <i>Massetognathus</i> . . . . .	56
7. Postcanines of <i>Exaeretodon</i> and <i>Gomphodontosuchus</i> . . . . .	58
V. DISTRIBUTION OF THE TRAVERSODONTIDAE . . . . .	60
VI. OCCLUSION IN <i>Tritylodon</i> AND THE ORIGIN OF THE TRITYLODONTIDAE . . . . .	61
VII. SUMMARY AND DISCUSSION . . . . .	64
VIII. ACKNOWLEDGEMENTS . . . . .	68
IX. REFERENCES . . . . .	69

## SYNOPSIS

Within the gomphodont cynodonts and their descendants, the tritylodontids, it is possible to trace the initiation and progressive improvement of postcanine occlusion and complex masticatory movements, beginning with primitive cynodonts in which mastication did *not* involve actual contact between matching upper and lower postcanine teeth. Occlusion in advanced cynodonts was functionally similar to that of primitive mammals with tribosphenic molars, and the mechanisms by which occlusion evolved in the two groups also appear to have been similar. In primitive gomphodont cynodonts and primitive mammals the crowns of occluding teeth had to be moulded by wear to produce accurately matching shearing surfaces; major features of the crown were thereby obliterated. In advanced members of both groups the topography of the crowns was modified so that only a little wear was needed to produce matching shearing planes.

A clear correlation appears to have existed between the occlusal relationships of the teeth of cynodonts and their replacement patterns. The enamel of cynodonts and tritylodontids was thin and apparently worn through rapidly, so that the structure of the crowns was soon destroyed; in order to compensate for this, worn gomphodont teeth were lost from the front of the row and new ones added behind.

The tritylodontids were probably derived from traversodont cynodonts. The longitudinally orientated shearing planes on the postcanine teeth became more numerous and the relative extent of the backward movement of the lower jaw during the final stages of mastication was progressively increased.

Three new species of traversodont cynodonts are named (*Scalenodon hirschsoni*, *S. attridgei*, *S. charigi*).

## INTRODUCTION

ACCURATE occlusion between cheek teeth with complex crown patterns is a mammalian character. It involves complicated relationships between the cusps, ridges and basins of occluding teeth and also mandibular movements that are seldom directly orthal during the final stages of the masticatory cycle (power stroke, Crompton & Hiiemae, 1969*a* & *b*), but are also partially transverse and forward. The relative amount of upward, forward and sideways movement during this phase of occlusion differs widely in the various mammalian orders. Many of the advanced cynodonts and tritylodontids independently developed occlusal patterns which in terms of function closely parallel those of later mammals. The purpose of this paper is to describe and discuss the development of postcanine occlusion in several groups of cynodonts, which are the most mammalian of the therapsid reptiles and the group from which mammals almost certainly arose. Although the cynodonts which had dental occlusion and which are discussed in this paper were not ancestral to mammals this study does throw some light on the mechanism involved in developing dental occlusion of the mammalian type.

Numerous authors have described and discussed the morphology of the teeth of therapsid reptiles; but few have described occlusal relationships, and except for one or two cases (Watson 1911, Parrington 1946) no attempt has been made to determine jaw movements during mastication or dynamic occlusion of the cheek teeth of this group. The functional aspects of mammalian occlusion also have been neglected, but recent papers on wear facets on the molars of living and extinct mammals (Butler, 1961; Mills, 1964, 1966, 1967; Kermack, Lees & Mussett, 1965; Crompton & Jenkins, 1967, 1968) and cineradiographic studies of mastication in a primitive mammal (Crompton & Hiiemäe, 1969, *a*, *b* & *c*) have provided a model with which to compare the dynamic occlusal relationships and possible jaw movements in cynodonts.

The infraorder Cynodontia (Fig. 1) arose in the late Permian, reached its greatest diversity in the Middle Trias and became extinct in the early part of the Late Trias. As will be shown below, the Tritylodontidae which survived until the Middle Jurassic can be considered as late survivors of the cynodonts. The Ictidosauria (*Diarthrognaethus*, *Pachygenelus* and *Trithelodon*) were probably also late survivors of the Cynodontia and a case can perhaps be made for including them within the cynodonts. The cynodonts are usually divided into the following families: the Procynosuchidae (I am including genera which have been placed in separate families by some authors, e.g. Silphedestidae, Dviniidae, Cynosauridae); the Galesauridae; the Cynognathidae; the Chiniquodontidae (this family probably includes most of the South American carnivorous cynodonts which have not yet been adequately described but which are at present being studied by Prof. A. S. Romer); the Trirachodontidae; the Diademodontidae; and the Traversodontidae. The interrelationships and time-spans of these families are shown in Figure 1. The last three families are commonly referred to as the gomphodont cynodonts and it is only in them that complex occlusion between upper and lower postcanine teeth occurred. Postcanine occlusion is present in the Ictidosauria, but it is not complex. The Traversodontidae were the most varied and abundant of the cynodonts and their remains have been discovered in the



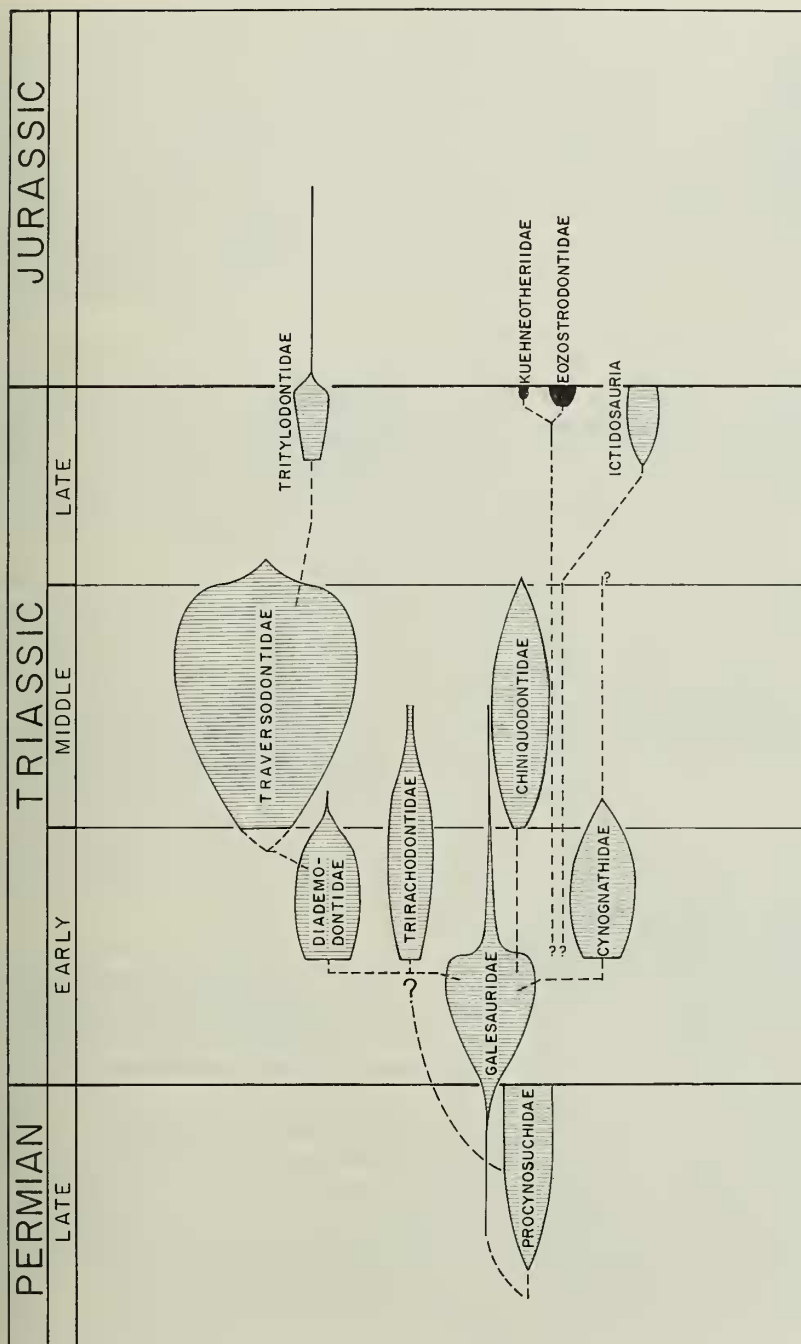


FIG. 1. Time-spans and interrelationships of the major cynodont families (vertically hatched). Also shown are the two earliest mammal families (black), the Kuehneotheriidae and the Eozostrodoniidae; apparently these were related to early cynodonts but no intermediate forms are known.

Middle Trias of East Africa, Late Trias of South Africa and in great abundance in the Trias of South America (see Crompton, 1955; Crompton & Ellenberger, 1957; Bonaparte, 1967a & b; Romer, 1967; and Sill, 1969 for pertinent literature). Numerous representatives of the remaining cynodont families have been found in the sedimentary rocks of the Karoo system of South Africa (Haughton & Brink, 1954 and Lehman, 1961 for pertinent literature), although they are also known from South America (Bonaparte, 1967a & b), China (Young, 1959 & 1961) and Russia (Tatarinov, 1968). Dental occlusion (i.e. tooth-to-tooth contact) is absent in the Procynosuchidae and Galesauridae but, as members of these families are ancestral to the later gomphodont cynodonts, their postcanine dentitions will be briefly considered.

## II. POSTCANINE DENTITION OF THE PROCYNOSUCHIDAE AND GALES SAURIDAE

The postcanine dentition of the Procynosuchidae is best known in the South African species *Leavachia duvenhagei*. In a recent review of procynosuchid literature Anderson (1968) suggested that *Procynosuchus*, *Galecranium* and *Galeophrys* were probably synonymous with *Leavachia*; the postcanine row of *Leavachia duvenhagei* consisted of 7 to 11 teeth according to the age of the individual. Alternate tooth replacement was observed in all specimens studied.

Mendrez (1967) figured the postcanines of an unidentified species of *Leavachia*. The crowns of postcanines from the middle of the row were circular in cross-section while those further back were longitudinally ovate (Fig. 2A). A large external cusp was present. On the internal edge of the crowns of both upper and lower teeth there was a series of small cusps, the most anterior and posterior of which were visible in external view; in this view therefore, the crown appeared to be tricuspid. In lateral view it could be seen that upper and lower postcanines alternated with one another; the centre of the lower tooth lay medial to the space between two upper teeth. The lower postcanines bit medial to the uppers but because there was no contact between upper and lower teeth matching shearing surfaces did not develop. The postcanines of these early cynodonts were therefore capable of gripping, puncturing and possibly crushing food but could not shear food efficiently.

The postcanine dentition of the aberrant procynosuchid *Dvinia prima* from the Russian Permian was described in detail by Tatarinov (1968), who placed the genus in a new family Dviniidae. The postcanine teeth were considerably more complex than those of *Leavachia*. The crowns of the upper postcanines ("molars") (Fig. 2B), were transversely ovate with a central cusp completely surrounded by several small cusps on the edge of the crown. Unlike those of *Leavachia* these cusps were present on the external edge of the crown as well as on the internal edge and the external cusps were slightly larger than the internals. The lower molars of *Dvinia prima* were similar to the uppers except that additional cusps were present in the centre of the crown medial to the main cusp. The postcanines of *Dvinia prima* could have been derived from those of *Leavachia* by the addition of a series of small external cusps. In *Dvinia* upper and lower canines did not occlude, i.e. there was no tooth-to-tooth contact, and the lower postcanines bit medial to the uppers. In these respects the teeth of *Dvinia* were superficially similar to those of *Leavachia*. Because

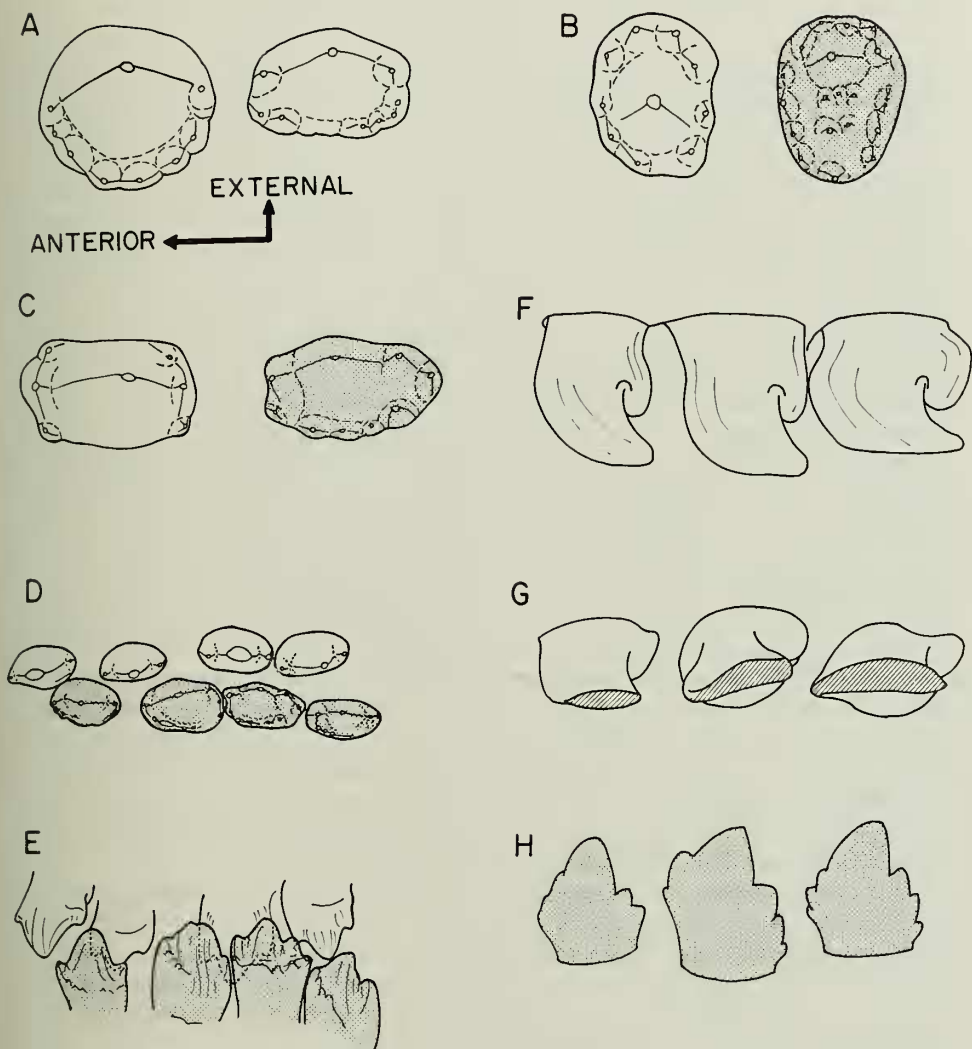


FIG. 2. Galesaurids and procynosuchids. Postcanine teeth. (In these and all other text-figures lower teeth are stippled, upper teeth are plain). A. *Leavachia*. Crown view of upper from middle and back of row. After Mendrez, 1967. B. *Dvinia prima*. Crown views of upper and lower. After Tatarinov, 1968. C. *Thrinaxodon*. Crown views of upper and lower. D. *Thrinaxodon*. Crown views of last four uppers and last four lowers. E. *Thrinaxodon*. Internal views of last four uppers and last four lowers. F. *Glochinodontoides gracilis*. External view of first three uppers. G. *Glochinodontoides gracilis*. Crown view of first three uppers. H. *Cynidiognathus*. External view of posterior lower postcanines. After Fourie, 1964.

the teeth were transversely ovate they appear to be similar to those of gomphodont cynodonts, but in the latter group crown-to-crown occlusion was present.

Several small Permian cynodont skulls have been described (e.g. *Protocynodon*, *Nanictosuchus*, *Nanictosaurus*, *Silphedestes*; see Haughton & Brink, 1954 for pertinent literature). These appear to have had postcanine teeth similar to those of the galesaurid *Thrinaxodon liorhinus* but until they have been adequately prepared and studied their taxonomic position will remain in doubt. It is possible that the fore-runners of the Galesauridae will be found among these little-known cynodonts.

The best-known member of the Galesauridae is *Thrinaxodon liorhinus*. Several undistorted skulls of this species have been prepared with acetic acid and the crown patterns and relationships of upper and lower postcanines studied in detail. The postcanine teeth did not occlude, replacement was alternate, their crowns were longitudinally ovate and both upper and lower crowns (especially the lowers) had a well developed internal cingulum which supported several cusps. In Fig. 2C, D & E and Plate 1 the postcanines are shown in crown and internal view. It will be seen that the upper and lower teeth tended to alternate with one another in position and that when the jaws were closed a considerable space separated the outer surface of the lower teeth and the inner surface of the upper teeth. All the specimens studied showed this. As in procynosuchids, the postcanines of *Thrinaxodon* did not develop matching wear facets on the internal surface of the uppers or external surface of the lowers, thus indicating that shearing did not take place; i.e., upper and lower teeth did not occlude with one another. Lateral movement of the lower jaws sufficient to enable upper and lower teeth to come into contact appears to have been prevented in both Galesauridae and Procynosuchidae by the strong transverse processes of the pterygoids and the large pits in the palate which accommodated the lower canines. *Tribolodon* from the younger *Cynognathus* zone had postcanine teeth similar to those of *Thrinaxodon* but the internal cingulum of the lower postcanines was reduced and, in the material available for study, I never observed more than two subsidiary cusps on the internal surface of either upper or lower postcanines.

The postcanine teeth of the remaining galesaurid genera, i.e. *Galesaurus*, *Glochionodon*, *Glochinodontoides*, *Platycraniellus* and *Cynosuchoides*, were distinct from those of *Thrinaxodon*. Upper and lower teeth (Fig. 2F, G; Plate 2) were apparently identical and were characterized by a strongly recurved main cusp with a sharp blade-like cusp behind and by a total absence of subsidiary cusps on the anterior or internal surfaces. The tip of the main cusp was worn but, as in *Thrinaxodon*, there were no matching shearing surfaces on upper and lower teeth. In a few specimens available for study teeth were being replaced, but there appears to have been a "break-down" of the alternate tooth-replacement pattern that characterized *Thrinaxodon* and the procynosuchids. The way in which these peculiar teeth functioned is not understood.

Galesauridae with teeth of this type may have been ancestral to the Cynognathidae or Chiniquodontidae. In *Cynognathus* and *Cynidiognathus* (Fourie, 1964) the postcanines usually lacked internal cingula; the main cusp was slightly recurved (Fig. 2H); and, depending upon the position of a postcanine in the tooth row, one, two or three anterior and posterior accessory cusps may have been present. In *Cyno-*



*gnathus* there was no obvious alternate replacement of the postcanines but the presence of matching wear facets on the external surface of the lowers and internal surface of the uppers shows that the teeth were used for shearing.

### III. POSTCANINE DENTITION OF THE DIADEMONTIDAE AND TRIRACHODONTIDAE

The earliest known cynodont to develop postcanines with a complex occlusal pattern was the gomphodont cynodont *Diademodon* from the early Trias of South Africa. The dentition has been described by Seeley (1895), Watson (1911), Broili & Schröder (1935) Brink (1955, 1957), Crompton (1955, 1963), Fourie (1963, 1964), Hopson (1971) and Ziegler (1969). The postcanine row was differentiated into two to six conical teeth in front; three to nine transversely widened gomphodont teeth in the middle; and two to five posterior teeth which range in crown structure from semi-gomphodont to fully sectorial (Fig. 3B). The number of teeth present depended upon the age of the individual. The upper gomphodont teeth were transversely ovate in crown view and wider than the corresponding lower teeth (Fig. 3A-C and Plate 2B) so that, when the teeth occluded, the inner and outer margins of the upper teeth overlapped the corresponding margins of the lowers (Fig. 14C). The alternate tooth replacement characteristic of *Thrinaxodon* did not occur in *Diademodon*; the details of replacement in the latter genus are not yet fully understood, but it was complex, not alternate, and apparently confined to the anterior and posterior regions of the postcanine row. At the front of the row sharp conical teeth replaced worn gomphodont teeth; at the back gomphodont teeth replaced either semi-gomphodont or sectorial teeth. Consequently the occlusal relationships between upper and lower gomphodont teeth were never disturbed by replacement in the middle of the row as would have been the case if replacement had been of the alternate pattern found in the earlier Galesauridae.

Ziegler (1969) concluded that there was probably no replacement at the back of the postcanine row of *Diademodon*, the pattern being essentially mammalian in that only the incisors, canines and anterior postcanines were replaced. His paper was based entirely upon published accounts of the dentition. Ziegler correctly pointed out inconsistencies both in my own and in other authors' attempts to interpret the tooth replacement pattern that was present in *Diademodon*, but his conclusions too are open to criticism and do not appear to be substantiated by the known material.

Dr. J. Hopson of the University of Chicago is at present preparing a manuscript on tooth replacement in *Diademodon* and Dr. J. Osborn of the Dept. of Oral Anatomy, Guys Hospital, London, is completing a manuscript on the order of tooth eruption and replacement in *Diademodon* and some early cynodonts. Because of this I do not wish to enter here into a full discussion of tooth replacement in *Diademodon* but would like to point out some problems raised by Dr. Ziegler's interpretation.

In the smallest known specimen of *Diademodon* (Kitching, private communication) the postcanine row contains two or three gomphodont teeth and is terminated by two or three teeth which appear to have been either semi-gomphodont or sectorial in structure. In slightly larger specimens (Brink, 1963b) the postcanine row contains five gomphodont teeth with three semi-gomphodont or sectorial teeth behind. In

still larger specimens (Crompton 1955, 1963b) up to seven gomphodont teeth are present with four or five semi-gomphodont or sectorial teeth behind. The *Diademodon* skulls of different sizes might be considered as different species but this is an extremely unlikely interpretation as many were found at one locality (Brink, 1963b); it is more reasonable to suppose that they represent growth stages of a single species (Kitching, 1968). Ziegler appears to have overlooked the size range of the available material of *Diademodon* and the fact that the postcanine row always ends in a series of teeth which become progressively more sectorial. It would be impossible to obtain the growth stages listed above without replacement at the back of the row. In the large series of jaws studied by Fourie (1964) there is clear evidence of the loss of some of the anterior conical postcanine teeth, and a specimen of *Diademodon* in East Berlin (Crompton, 1963b) clearly documents the replacement of the most anterior gomphodont tooth by a conical tooth. In 1955 I interpreted a longitudinally ovate opening below an unerupted posterior postcanine tooth of *Diademodon* as an alveolus, but it seems that Ziegler does not accept this as evidence of replacement of a sectorial tooth by gomphodont tooth at the back of the postcanine row.

*Diademodon* is closely related to other gomphodont cynodonts such as *Trirachodon*, *Cricodon*, *Scalenodon* and a new and as yet undescribed and unnamed reptile from the Ntawere Formation of the Luangwa Valley (Zambia). In a *Trirachodon* skull prepared by Dr. F. R. Parrington and figured by myself (1963a) there is clear evidence of the replacement of the sectorial teeth at the end of the postcanine row by gomphodont teeth. In a late survivor of the Trirachodontidae, *Cricodon* (Crompton, 1955), a longitudinally ovate foramen containing the root of a sectorial tooth lies below an unerupted gomphodont tooth; this foramen is similar in shape and position to that found in *Diademodon* but was clearly an alveolus and not a gubernacular canal. In some species of *Scalenodon* the postcanine row is terminated by small gomphodont teeth; unerupted larger gomphodont teeth lay above the small teeth and would presumably have replaced them later. This evidence, derived from growth stages of *Diademodon* and from related forms that have been figured or studied in South Africa, suggests that the posterior postcanine teeth were replaced during growth. *Diademodon* may eventually have reached a mature stage when replacement ceased in the postcanine series and this may explain why in several of the larger individuals there is no clear evidence of replacement at the back of the row. Ziegler is perhaps unaware that most of the available *Diademodon* material is poorly preserved and has undergone little or no development; careful preparation of the existing material will probably show teeth that were in the process of being replaced at the time of death.

The important points concerning *Diademodon* are that gomphodont teeth were lost in front (or were replaced by conical teeth); that they were added behind (by the replacement of existing semi-gomphodont or sectorial teeth); and that there is no evidence of replacement of gomphodont teeth by gomphodont teeth. Consequently, a series of gomphodont teeth always shows a progressive increase in wear towards the front; this is because of the occlusal relationships of the postcanine teeth. The replacement patterns of teeth in gomphodont cynodonts ensured that in *Diademodon* a fresh supply of cusped gomphodont teeth were added during growth and that in



the later forms a fresh supply of teeth with deep shearing planes were added. In gomphodonts the enamel covering the crowns of the teeth appears to have been thin and perhaps soft, so that the structure of the crown was soon worn away and the teeth were perhaps replaced more rapidly than in mammals.

The exact order of tooth replacement occurring in the ontogeny of *Diademodon* is not fully understood; it is hoped that further work on material already available will clarify this process and meet the objections raised by Dr. Ziegler.

Crown views of unworn upper and lower gomphodont teeth of *Diademodon* are given in Fig. 3A and Plate 2. The upper crowns were transversely ovate whereas the lower crowns tended to be more circular. The upper crown was dominated by an external main cusp from which a well-defined ridge ran directly forwards, bearing two or three subsidiary cusps which became smaller towards the front; another ridge, ill-defined and slightly crenulate, ran backwards from the tip of the external main

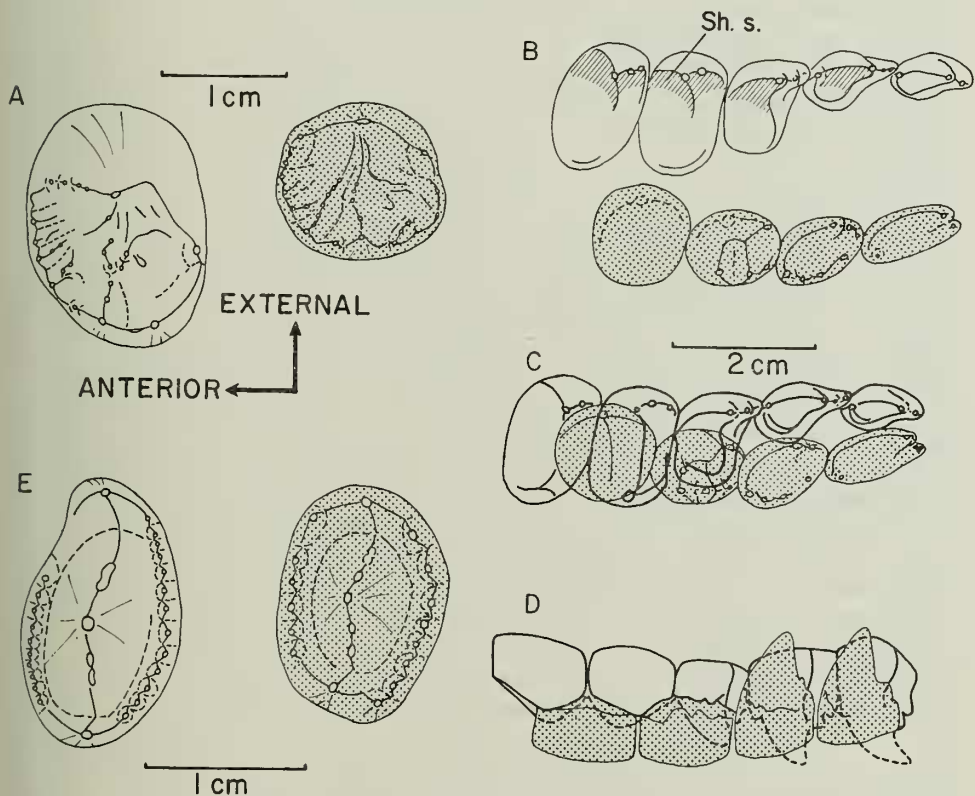


FIG. 3. *Diademodontids* and *trirachodontids*. Postcanine teeth. A. *Diademodon*. Crown view of typical upper and lower gomphodont teeth. B. *Diademodon*. Crown views of last five uppers and last four lowers to show shearing surfaces produced by wear. C. As in B, but superimposed as when occluded. D. As in C, occluded, but in internal view. E. *Cricodon*. Crown views of typical upper and lower. For key to abbreviations see p. 69.

cuspl. The internal edge of the crown was dominated by two cusps, the anterior and posterior internal cusps, which, although smaller than the external cusp, were almost as high. The anterior edge of the crown bore a series of four or five small cusps which tended to become bigger towards the mid-line. The posterior edge supported one or two well-defined cusps of unequal size and a series of small cusplules or crenulations. A series of crenulated ridges radiated from the centre of the crown towards both the anterior and the internal cusps, with shallow valleys or basins lying between. A series of three or four smaller ridges radiated from the base of the external main cusp towards the centre of the crown to terminate in an ill-defined high area which supported a series of small cusps and which, together with the ridges radiating from the external and internal cusps, formed an ill-defined transverse ridge. A shallow occlusal basin was formed between the transverse ridges of two consecutive teeth, the ridge running backwards from the main cusp of the anterior tooth and the ridge running forwards from the main cusp of the posterior tooth.

The crowns of the lower gomphodont teeth of *Diademodon* were similar to those of the upper. Each had an external main cusp from which a ridge ran backwards, supporting one or two cusps which became smaller towards the back. A weak ridge ran forwards from the main cusp to terminate in a prominent cusp on the antero-external edge of the crown. A prominent cusp was present on the middle of the internal edge of the crown connected with the base of the main cusp by a ridge running transversely across the crown. Ridges supporting smaller cusplules radiated medially from the main cusp. A series of cusps was present on the anterior edge of the crown, from each of which a ridge ran backwards; they became bigger towards the mid-line. The central region of the crown was relatively high and flat.

The unworn crowns appear to have been capable of crushing and puncturing food and it seems that the details of the crown pattern were quickly worn away in most *Diademodon* specimens. The enamel of *Diademodon* postcanines was extremely thin. The external main cusp of the lowers pounded into the basin formed between two adjoining upper postcanines (Figs 3C & 14) and, as wear proceeded, insignificant vertical shearing planes (Sh.s.) were developed between the external surface of the lower cusp and the internal surfaces of the ridges running forwards and backwards from the external main cusps of two adjoining upper teeth (Figs 3B & 14). As the external main cusps were worn down, these planes were lost and the anterior gomphodont teeth were reduced to featureless nubbins of dentine. In several primitive mammals, e.g. *Eozostrodon* and *Tinodon* (Crompton & Jenkins, 1967, 1968), occlusal planes were established by destroying major features of the crown.

The gomphodont postcanine teeth of *Diademodon* were followed by a series of three or four teeth which became progressively more sectorial towards the back, that is, the inner extension of the crown became progressively smaller. During occlusion the main cusp of the first semi-gomphodont lower tooth met the crown of the matching semi-gomphodont upper tooth internal to the main cusp of the latter and slightly behind the gap between the last gomphodont tooth and first semi-gomphodont tooth. The occlusal details of the posterior postcanines are illustrated in crown view in Fig. 3C and in internal view in Fig. 3D. As the lower jaw closed, shearing was possible between the outer surface of the main cusp of the lower semi-

gomphodont tooth and the inner surface of the main cusp of the upper. However, as the tip of the main cusp of the lower tooth abutted against the occlusal surface of the internal extension of the corresponding upper cusp, it was rapidly worn down and its shearing function reduced. In the more advanced traversodonts the lower jaw was pulled backwards as the teeth came into occlusion; this postero-dorsally directed power stroke may have been initiated in *Diademodon*.

The postcanine dentition of *Diademodon* showed a significant advance beyond the galesaurid condition.<sup>1</sup> The lower teeth lay directly below the crowns of the upper rather than internal to them. The cusps of upper and lower postcanines could therefore be used more effectively for puncturing and crushing food. In addition, matching vertical shearing surfaces were present on both the gomphodont series and the sectorial series of postcanine teeth; these were rapidly obliterated by wear but this was compensated for by the type of tooth replacement present in *Diademodon* which ensured that new gomphodont and sectorial teeth either replaced existing teeth at the back of the row or were added thereto. The gomphodont postcanines of *Diademodon* may be derived from those of early galesaurids or procynosuchids by widening the teeth in a lingual direction. The Lower Triassic cynodonts *Pascualgnathus* and *Andescynodon* recently discovered in South America by Bonaparte (1967b) may throw considerable light on the evolution of the *Diademodon* type of postcanine tooth from those of earlier cynodonts.

The postcanine teeth of *Trirachodon* of the South African Lower Trias and of *Cricodon* of the East African Middle Trias were slightly different from those of *Diademodon*. The postcanine row consisted of six or seven transversely ovate gomphodont teeth with two or three sectorial teeth behind. There was a sharp break between these two series; the transitional zone present in *Diademodon*, where the teeth become progressively more sectorial towards the back, was absent. The upper and lower gomphodont teeth in *Trirachodon* (Fig. 14) and *Cricodon* (Fig. 3E and Plate 3) had three main cusps, an external, a central and an internal arranged to form a prominent transverse ridge across the crown. The anterior and posterior margins of the crown each bore a row of small cusps. The faint ridges which ran forwards and backwards from the external and internal main cusps of the uppers were not worn by the lowers to produce the vertical shearing surface seen in *Diademodon*; some degree of shearing may have been present between the sectorial teeth, but these were so small in comparison with the gomphodont teeth that it could not have been significant. The gomphodont teeth were presumably used to puncture and crush. The transverse ridges of the upper and lower teeth alternated with one another during occlusion but the wear facets suggest that they could not have sheared effectively.

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<sup>1</sup>I have assumed that *Diademodon* was derived from a galesaurid similar to *Thrinaxodon*. This assumption is based upon the similarity of the sectorial teeth of *Diademodon* to the teeth of *Thrinaxodon* and upon the anteroposterior alignment of the cusps on the external edge of the upper teeth of *Diademodon*. It is based also on the fact that galesaurids were the dominant cynodonts of the *Lystrosaurus* zone and that as a family they represent a distinct advance over the procynosuchids of the earlier *Kistecephalus* zone. However, some or all of the gomphodont cynodonts may have arisen directly from the Procynosuchidae (Bonaparte, 1963); this would explain the single external cusp on the gomphodont teeth of the Trirachodontidae.

In the Trirachodontidae there was no alternate tooth replacement and, as in *Diademodon*, new gomphodont teeth were added behind to replace sectorial teeth.

#### IV. POSTCANINE DENTITION OF THE TRAVERSODONTIDAE

Until recently relatively little was known about Middle to Late Triassic therapsids (Crompton 1955, 1963B); recent work in South America, South Africa and East Africa, however, has led to the discovery of numerous therapsid remains, most of which have still to be described. It is now clear that the gomphodont cynodonts of the family Traversodontidae were the dominant cynodonts during the Middle Trias and early part of the Late Trias. The basic pattern of the crowns of the postcanine teeth of the traversodontids is characteristic of the group and separates it very clearly from the earlier gomphodont cynodonts. Relatively minor differences in the dentition and occlusal relations distinguish the genera of traversodontid cynodonts from each other, the structure of the postcanines providing a useful key for identifying genera and species and for determining the relationships and evolutionary history of the group. Like those of diademodontids, the postcanines of traversodontids were subjected to severe wear which in most cases eventually obliterated all details of the crown pattern. It will be shown below that the wear of the crowns of traversodontid postcanines resulted from a combination of complex occlusal relationships and jaw movements. The occlusion of traversodontid postcanines closely paralleled that of primitive mammals with tribosphenic molars. The abundance and diversity of traversodontids during Middle Triassic times may have been partly due to their highly evolved masticatory apparatus.

In an earlier paper (Crompton 1955) three new genera of cynodonts (*Scalenodon*, *Cricodon* and *Aleodon*) and several indeterminate remains were described from the Manda Formation of Tanzania. No attempt was made to classify them above the generic level. Romer (1967) has recently revised the classification of gomphodont cynodonts; it is now apparent that *Scalenodon angustifrons* and the isolated maxilla with two teeth which I compared with the South American genus *Gomphodontosuchus* should both be included in the family Traversodontidae, while *Aleodon brachyrhamphus* is clearly not a traversodontid and *Cricodon metabolus* appears to have been a surviving member of the Trirachodontidae. This accords with a view expressed by Bonaparte (1963). Subsequently Brink (1963a) described a gomphodont, *Luangwa drysdalli*, from the Ntawere Formation of Zambia; it is not well preserved and the occlusal aspects of the teeth are not known, but it appears to have been closely related to *Scalenodon angustifrons*, if not actually identical. In 1963 the British Museum (Natural History)—University of London Joint Palaeontological Expedition (Attridge, Ball, Charig & Cox, 1964) collected additional material from the Ntawere Formation of Zambia and the Manda Formation of Tanzania; at least one new genus and two new species of traversodontid cynodonts were discovered as well as additional specimens of *Scalenodon angustifrons* and *Aleodon brachyrhamphus*. I hope to give a full description of this new material in a later publication. Meanwhile, because the postcanine teeth of all the East African traversodontids (including the new material) are discussed below, the new specimens have been named and briefly described in order to avoid future confusion.



1. Description of three new species of *Scalenodon*  
from the Middle Trias of East Africa

Family **TRAVERSODONTIDAE** von Huene 1936

Genus **SCALENODON** Crompton 1955

TYPE-SPECIES. *Trirachodon angustifrons* Parrington 1946.

Since I first described *Scalenodon* (Crompton 1955 : 647) other genera have been discovered in East Africa, South Africa and South America which are closely related to it. Because of this the original diagnosis given for *Scalenodon* is no longer applicable, several of the supposedly diagnostic features mentioned having subsequently proved to be diagnostic of the family Traversodontidae as a whole rather than of the genus *Scalenodon* in particular. A revised diagnosis for *Scalenodon* is therefore given below.

This diagnosis is based entirely upon the characters of the upper postcanine teeth; it does not include features of the lower postcanine dentition because the latter is not known in all species of the genus. A detailed description of the rest of the skulls and skeletons of the several species of *Scalenodon* is now projected; this may necessitate some revision of the classification suggested in this paper.

DIAGNOSIS. Small to medium-sized traversodontid cynodonts in which the upper postcanine teeth are transversely ovate; the external margin of the crown is gently convex; two main cusps are present (external and internal), the latter lying at the internal end of a prominent transverse ridge which usually supports an additional (central) cusp; small antero-external and antero-internal cusps are occasionally present; the inner surfaces of the external cusps form a vertical, antero-posteriorly aligned shearing surface, towards which the accessory cusp does not contribute substantially (contrast South American traversodontids); anterior and posterior cingula are present; during the power stroke of occlusion the backward movement of the lower jaw was limited so that matching transverse ridges, upper and lower, were never drawn across one another.

COMMENTS. The upper postcanines of the four species of *Scalenodon* show some striking similarities to those of various genera of traversodontid cynodonts from South America. The type-material from both continents is at present being studied in order to determine, if possible, whether those similarities are due merely to convergence or to a closer phylogenetic relationship than is indicated by the present classification.

*S. angustifrons* (Parrington). Material of this species includes not only the holotype (Cambridge University Museum of Zoology, Ruhuhu Field Catalogue no. 120B) but also a number of other specimens which I referred to it when proposing the genus (Crompton 1955). Details of horizon and localities are given and discussed in the same work. Now that three new species of *Scalenodon* have been recognized (see below) it is possible to give a specific diagnosis for *S. angustifrons*. The diagnostic characters of all four species are compared in Table 1. Note also that in *S. angustifrons* there is a ridge of small cuspules on the outer surface of the main cusp of the upper postcanines.

TABLE I

	<i>S. angustifrons</i>	<i>S. hirschsoni</i>	<i>S. altridgei</i>	<i>S. charigi</i>
Text-figure:	4C	7A	10A	10C
position of tooth-row:	curving away from mid-line posteriorly	nearly parallel to mid-line	curving away from mid-line posteriorly	unknown
setting of teeth in maxilla:	not oblique	not oblique	oblique	very oblique
shape of gomphodont teeth in crown view:	inner region never wider than outer	more rectangular than in <i>S. angustifrons</i>	inner region wider than outer	anterior and posterior margins roughly parallel
transverse ridge:	behind middle of tooth, high with steep anterior and posterior walls, supports external and central cusps	more posterior in position than in <i>S. angustifrons</i> , lower, supports external and central cusps	still more posterior in position, supports external and central cusps	forms part of posterior edge of crown, central cusp appears to be absent
external and internal anterior accessory cusps:	absent	present	external small, internal large	both large, connected by high anterior wall
anterior cingulum:	poorly developed	well developed	well developed forms cuspidate anterior wall in posterior postcanines	well developed, forms non-cuspidate anterior wall
posterior cingulum:	poorly developed	well developed	well developed but less prominent than in <i>S. hirschsoni</i>	poorly developed



*Scalenodon hirschsoni* sp. nov.

Plate 5; Text-figs 7-9

DERIVATION OF NAME. In honour of Dr B. Hirschson, who was a member of the British Museum (Natural History)—University of London Joint Palaeontological Expedition to Northern Rhodesia and Tanganyika, 1963, and who has done so much to help vertebrate palaeontologists and archaeologists working in southern Africa.

MATERIAL. Only the holotype in the British Museum (Natural History), Pal. Dept. regd. no. R. 8577. Field catalogue no. U12/3/26. Partial skull with well-preserved postcanine teeth.

HORIZON. Manda Formation (Middle Trias, probably Anisian).

LOCALITY. Ruhuhu Valley, S.W. Tanzania: Locality U12 of the B.M.(N.H.)—University of London Joint Expedition, 1963. Between the Hiasi and Njalila streams, just south of the Rutukira River; the most northerly of the Expedition's localities west of the Njalila.

DESCRIPTION. See Table 1 for diagnostic characters. Note also that the incisors and canines, both upper and lower, are procumbent. The postcanines are described in greater detail on p. 49.

*Scalenodon attridgei* sp. nov.

Plate 6; Text-figs 10A, B

DERIVATION OF NAME. In honour of Mr John Attridge, of Birkbeck College, London, who was a member of the British Museum (Natural History)—University of London Joint Palaeontological Expedition to Northern Rhodesia and Tanganyika, 1963, and who made many of the discoveries of that expedition, including the unique specimen of this species.

MATERIAL. Only the holotype in the British Museum (Natural History), Pal. Dept. regd. no. R. 8578. Field catalogue no. U2/2. A beautifully preserved snout with complete upper dentition; probably a young individual.

HORIZON. Manda Formation (Middle Trias, probably Anisian).

LOCALITY. Ruhuhu Valley, S.W. Tanzania; Locality U2 of the B.M.(N.H.)—University of London Joint Expedition, 1963. Immediately next to the Peramiho-Litumba dirt road, on its left (south-western) side; low in the K8, before the Expedition's turn-off to Njalila and Mkongoleko, and probably only about a mile before the K7 boundary.

DESCRIPTION. See Table 1 for diagnostic characters. Note also that the anterior edge of the unworn crown of the upper postcanines bears a row of five distinct cusps, of which the innermost is the largest. The postcanines are described in greater detail on p. 53.

*Scalenodon charigi* sp. nov.

Text-fig. 10C

DERIVATION OF NAME. In honour of Dr Alan J. Charig, Curator of Fossil Reptiles in the British Museum (Natural History), who initiated and participated in the B.M.(N.H.)—University of London Joint Palaeontological Expedition to Northern Rhodesia and Tanganyika in 1963.

MATERIAL. Only the holotype in the Cambridge University Museum of Zoology, Ruhuhu Field Catalogue no. 136. Part of a left maxilla in which two postcanine teeth are preserved.

HORIZON. Manda Formation (Middle Trias, probably Anisian).

LOCALITY. Ruhuhu Valley, S.W. Tanzania; Locality B26 of Stockley (1932 : 620). Gingama, south of the Ruhuhu River.

DESCRIPTION. See Table 1 for diagnostic characters. Note also that the central main cusp of the upper postcanines *appears* to be absent (this part of the tooth is damaged).

COMMENTS. This specimen was described and figured by Crompton (1955 : 659–660, fig. 14E), who compared it with the Brazilian species *Gomphodontosuchus brasiliensis*. It is now clear that its postcanine teeth are distinct from those of the other Ruhuhu traversodontids; the antero-external and internal accessory cusps are better developed than in the other East African forms, the antero-external forming part of a vertical shearing surface. It is therefore desirable, despite the smallness of the preserved portion, to base a new species on this specimen.

*S. charigi* is similar in some respects to *Gomphodontosuchus brasiliensis* but is nevertheless distinct from that too. The postcanine teeth, though smaller, closely resemble those of the South American genera *Exaeretodon* and *Gomphodontosuchus*; the matching transverse ridges, however, did not cross one another during the power stroke of occlusion as they did in *Exaeretodon* and *Massetognathus*.

## 2. Occlusion and jaw movements in the primitive traversodontid *Scalenodon angustifrons*

The most primitive traversodontid postcanines known are those of *Scalenodon angustifrons*.<sup>2</sup> Although the dentition of this species has been described in detail (Crompton 1955), the new material discovered by the 1963 Joint Expedition has revealed many features of the postcanines and their occlusion which were not dealt with before.

Fig. 4 shows three views of typical upper and lower postcanines of *S. angustifrons*; stereo-photographs are given in Plate 4.

<sup>2</sup>If *Andescynodon* and *Pascualgnathus* described by Bonaparte (1966, 1967b) are considered as traversodontids, then these should be regarded as the most primitive members of the family. I, however, should prefer to place them in the Diademodontidae.

Upper teeth. These consisted essentially of three cusps arranged to form a transverse row, the central cusp being nearer the inner side of the crown. The internal (i.c.u.) and central (c.c.u.) cusps formed a high, prominent transverse ridge (t.r.) with anterior and posterior surfaces nearly vertical; a deep embayment (e.) separated this ridge from the external cusp (e.c.u.). A sharp ridge (a.r.) running forwards from the apex of the external cusp had a nearly vertical inner face which formed the outer border of a deep valley (a.v.) in the anterior surface of the tooth,

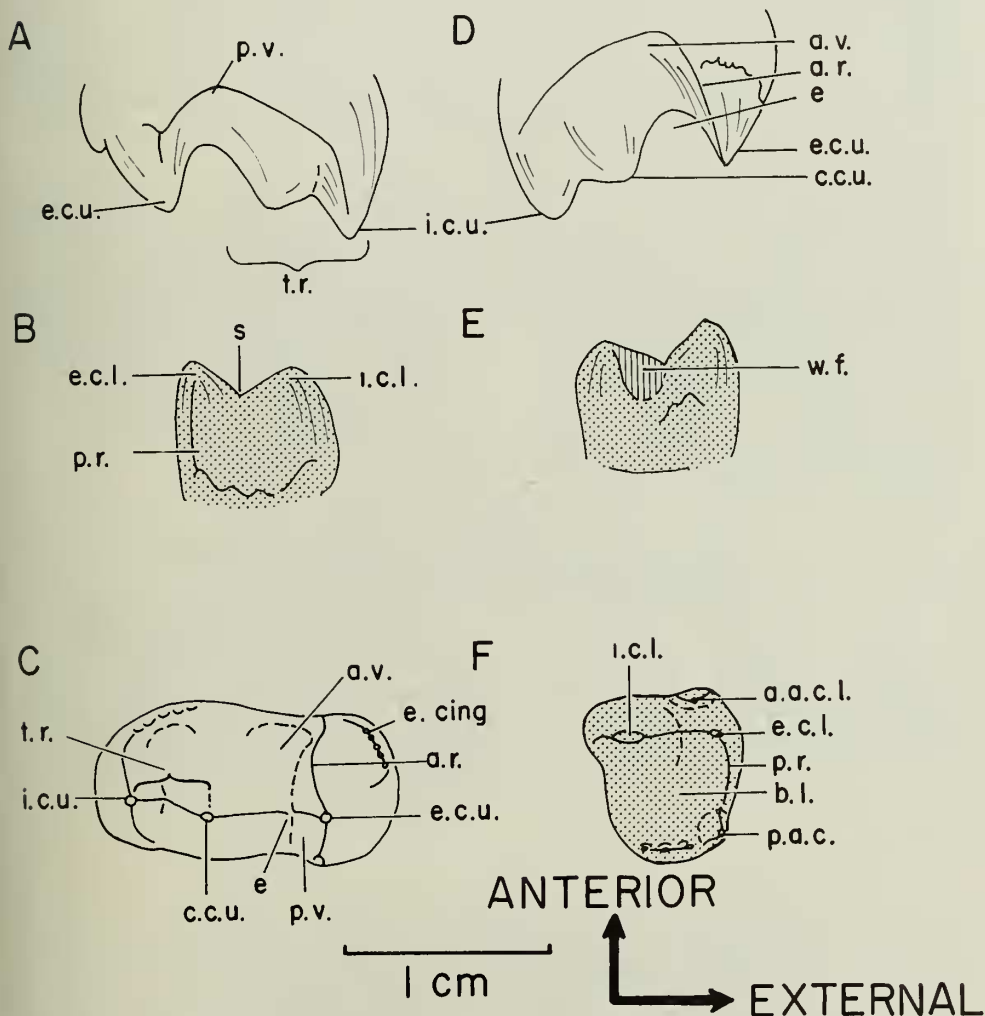


FIG. 4. *Scalenodon angustifrons*. Postcanine teeth. A. Posterior view of upper. B. Posterior view of lower. C. Crown view of upper. D. Anterior view of upper. E. Anterior view of lower. F. Crown view of lower. For key to abbreviations see p.69

immediately in front of the embayment between the external and central cusp (see Fig. 4D). A smaller, less well defined valley (p.v.) occupied a corresponding position behind the transverse ridge. The anterior valley of one postcanine and the posterior valley of the preceding tooth together formed a deep occlusal basin with high antero-posteriorly aligned shearing surfaces.

Lower teeth. The crown of a lower postcanine of *S. angustifrons* consisted of two high anterior cusps, the external (e.c.l.) being higher than the internal (i.c.l.); a high ridge ran backwards along the outer surface of the crown (p.r.) from the apex of the external cusp, its outer surface being more or less vertical. The external and internal cusps were connected by a transverse ridge which dipped down to a saddle between them; the anterior surface of this ridge was nearly vertical. A deep basin (b.l.) lay behind the two main cusps, rimmed posteriorly by a row of small cuspules of which the outermost (p.a.c.) was the largest. A small anterior accessory cusp (a.a.c.l.) was present on the anterior surface of the crown.

OCCLUSION. In Fig. 6 several opposing postcanines are shown in crown view and oblique internal view at the beginning of dynamic occlusion (A, B, respectively) and at the end (C, D). At the beginning of dynamic occlusion the anterior surface of the transverse ridge formed by the two main cusps of the lower tooth sheared past the posterior surface of the transverse ridge formed by the central and internal main cusps of the preceding upper tooth. (In Fig. 6B lower postcanine 6 is shearing

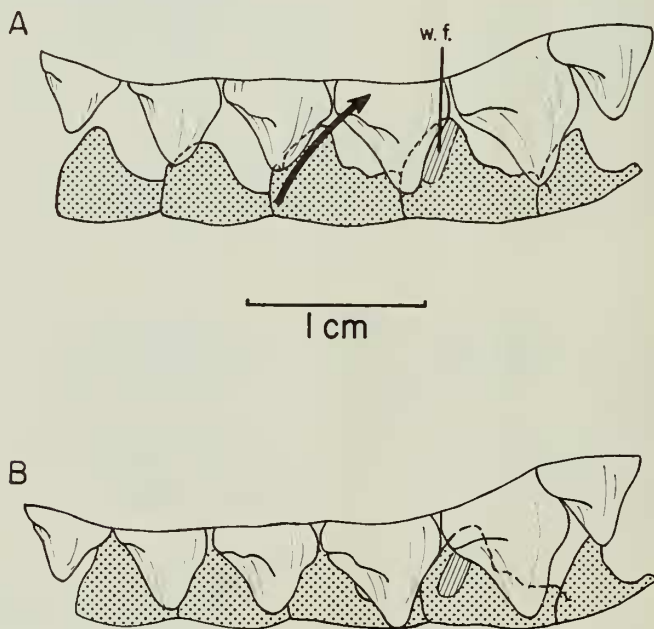


FIG. 5. *Scalenodon angustifrons*. Lateral views of postcanine teeth, showing the postero-dorsal direction of the power stroke. A. At the beginning of dynamic occlusion. B. At the end of dynamic occlusion.

against upper postcanine 5). This produced wear facets on the front of the transverse ridge of the lowers and on the back of the transverse ridge of the uppers. The central cusp of the upper tooth fitted into a groove on the anterior surface of the lower tooth between the two main cusps. The outer surface of the external main cusp of the lower tooth sheared past the posterior portion of the vertical internal surface of the external main cusp of the preceding upper postcanine; the position of the postcanines at the beginning of dynamic occlusion as seen in lateral view is given in Fig. 5A, which shows the resulting striations (w.f.) on the outer surface of the external main cusp of the lowers. As the jaws continued to close (Figs 5B and 6D) the lower jaw moved slightly backwards as well as upwards so that the external surface of the lowers sheared past the anterior portion of the vertical internal surface of the external cusp of the corresponding upper postcanine tooth. The arrows in

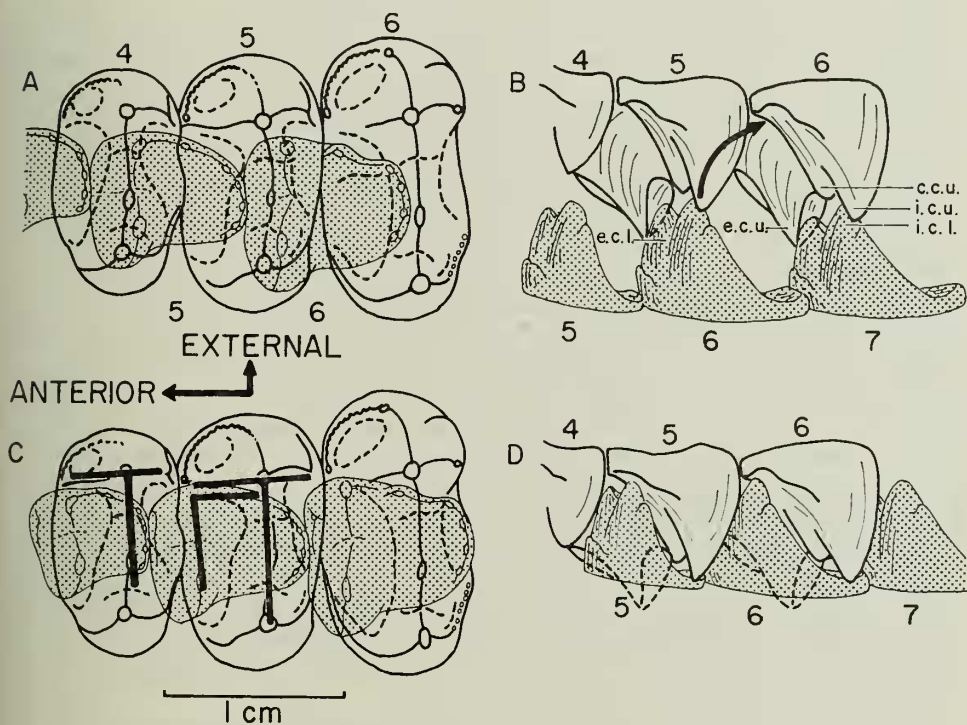


FIG. 6. *Scalenodon angustifrons*. Details of tooth occlusion. The numbers 4 to 7 indicate the positions of the teeth in the postcanine series. A. Crown views of the postcanines at the beginning of dynamic occlusion, with upper and lowers superimposed. B. Oblique internal view of the same. The heavy arrow indicates the passage of the tip of the internal main cusp of the lower teeth during dynamic occlusion. C. Crown views of the postcanines at the end of dynamic occlusion, with uppers and lowers superimposed. The main transverse and longitudinal shearing surfaces are drawn in heavy lines. D. Oblique internal view of the same. For key to abbreviations see p. 69.



Figs 6B and 5A indicate the direction of movement of a single lower postcanine during the final stages ("power stroke") of occlusion. The posterior surface of the external cusp of the lower tooth and the anterior surface of the external cusp of the corresponding upper formed two opposing crescents when seen in lateral view (Fig. 5A). Such an arrangement is ideal for cutting provided that the lower jaws moved slightly backwards during occlusion. An analogous arrangement typified the shearing surfaces of tribosphenic molars (Crompton & Hiiemäe, 1969b). When the postcanines of *S. angustifrons* were in tight occlusion (Fig. 6, C and D) the external main cusp of a lower postcanine lay in the valley (Fig. 4D, a.v.) in the anterior surface of the corresponding upper postcanine and the central cusp of the upper lay above the posterior basin of the lower. The dentition of *S. angustifrons* was characterized also by the addition of new gomphodont teeth with shearing surfaces behind and by the loss of worn postcanines in front. The replacement pattern was similar to but simpler than that of *Diademodon*.

The occlusal pattern of *S. angustifrons* represented a distinct advance over that of *Diademodon*. Not only were transversely orientated shearing planes added, but the occlusal basin of the upper postcanines was considerably deepened by the development of deep valleys immediately internal to the external main cusp. Consequently the tip of the main cusp of the lower postcanine was not worn down as rapidly as it was in *Diademodon*, where it abutted directly against the crown surface of the occluding tooth. Deepening the occlusal basin also increased the height of the shearing surfaces.

The postcanines of *S. angustifrons* therefore consisted essentially of a series of transversely and longitudinally orientated shearing planes. The positions of these shearing planes on upper and lower postcanines are indicated by heavy lines on Fig. 6C. Occlusion in other traversodontid cynodonts and tritylodontids was basically a modification of the arrangement that was present in *Scalenodon angustifrons*. The tips of the cusps were used for puncturing, the sides of several of the cusps for shearing and the posterior heel of the lower posterior postcanines provided a firm basin for crushing, analogous to the talonid basin of the tribosphenic molar. The postcanines of *S. angustifrons* were therefore functionally similar to the tribosphenic molars of primitive mammals. In mammals with tribosphenic molars and in some of the insectivores and herbivores with more specialized molars the jaw moves not only vertically during occlusion but also transversely and forwards in order to utilize a series of shearing plates. In *S. angustifrons* the mandible moved vertically and slightly *posteriorly* during occlusion and thereby also utilized a series of shearing planes.

It is generally assumed that in primitive cynodonts the tympanic membrane was partially attached to the posterior surface of the quadrate (see Hopson, 1966 for a complete review of this problem). The posterior movement of the jaw during dynamic occlusion in *S. angustifrons* was apparently too great to be accommodated within the available space between the glenoid of the articular and the condyle of the quadrate. Parrington (1946) suggested that in *Thrinaxodon* and later cynodonts the quadrate itself must have been capable of antero-posterior movement but recognized that such movement would have torn or stretched the small tympanic membrane



because the stapes rested against the quadrate. In a new skull of *S. angustifrons* (B.M.(N.H.) R. 8579), discovered in 1963 in Tanzania, it can be seen that the quadrate was held in a groove in the squamosal and could slide both downwards and forwards; the amount of movement of which it was capable appears to have been sufficient to have allowed the mandible to be pulled backwards a little during the final stages of dental occlusion. Kemp (1969), following on the earlier work of Parrington (1955), has shown that the quadrate was extremely mobile in gorgonopsians too so that, despite the firm junction between the articular and the quadrate, the mandible was capable of antero-posterior movements during mastication; a mobile quadrate was presumably present in all cynodonts and therocephalians. In *S. angustifrons* the external auditory meatus presumably lay in a groove of the squamosal and, as Parrington (1946) has shown, the groove was terminated by a semicircular lip which supported the tympanic membrane without involving the posterior surface of the quadrate. Movement of the quadrate would therefore not have involved the tympanic membrane directly, but this does not solve the problem completely as the stapes was presumably in contact with both tympanic membrane and quadrate, and stapes and quadrate may have moved together. Unfortunately the relationship between the stapes and the quadrate of advanced cynodonts is not well known, but the removal of the tympanic membrane contact from the quadrate to the squamosal in primitive traversodontids may be related to the antero-posterior movements of the mandible which appear to have taken place during occlusion.

The postcanine tooth rows of *S. angustifrons* diverged backwards. Consequently antero-posteriorly aligned cutting surfaces of opposing teeth would have tended to separate during extensive backward movement of the lower jaw and for this reason the amount of antero-posterior movement during occlusion in *S. angustifrons* was probably small. It is doubtful whether the jaw could have swung far enough laterally to retain contact on one side. A mobile mandibular symphysis would have overcome this limitation, but the nature of the fossil material suggests that the two rami were firmly united. The fossilized remains of *S. angustifrons* consist of numerous fragments, indicating that the skeletons of this animal were usually scattered and broken before fossilization; despite this the mandibular rami are usually found fused at the symphysis, as would not be expected had the symphysis been mobile during life. By contrast, the mandibular rami of tritylodontids and early mammals are seldom if ever preserved fused at the symphysis, which suggests that the latter was mobile. Szalay (1969) has argued that primitive primates too had a mobile symphysis because Palaeocene primate mandibles are usually preserved separated.

### 3. Occlusion and jaw movements in *Scalenodon hirschsoni*

The only known specimen of *S. hirschsoni* is ideal for the study of occlusion because it yielded to preparation with acetic acid; the lower jaw was thereby freed from the remainder of the skull. It was possible to study details of the structure of the teeth, the wear facets and occlusal relationships. Among the features of this species which clearly separate it from *S. angustifrons* are that the upper incisors and lower canines

are slightly procumbent and that the postcanine rows are nearly parallel to one another, the last postcanine lying immediately in front of the transverse process of the pterygoid. The basic structure of the crowns of the postcanines (Figs 7A, B, 8; Plate 5) is essentially the same as that of *S. angustifrons*. The crowns of the upper postcanines are relatively longer antero-posteriorly than those of *S. angustifrons* and the portion of the crown lying in front of the transverse ridge is considerably wider

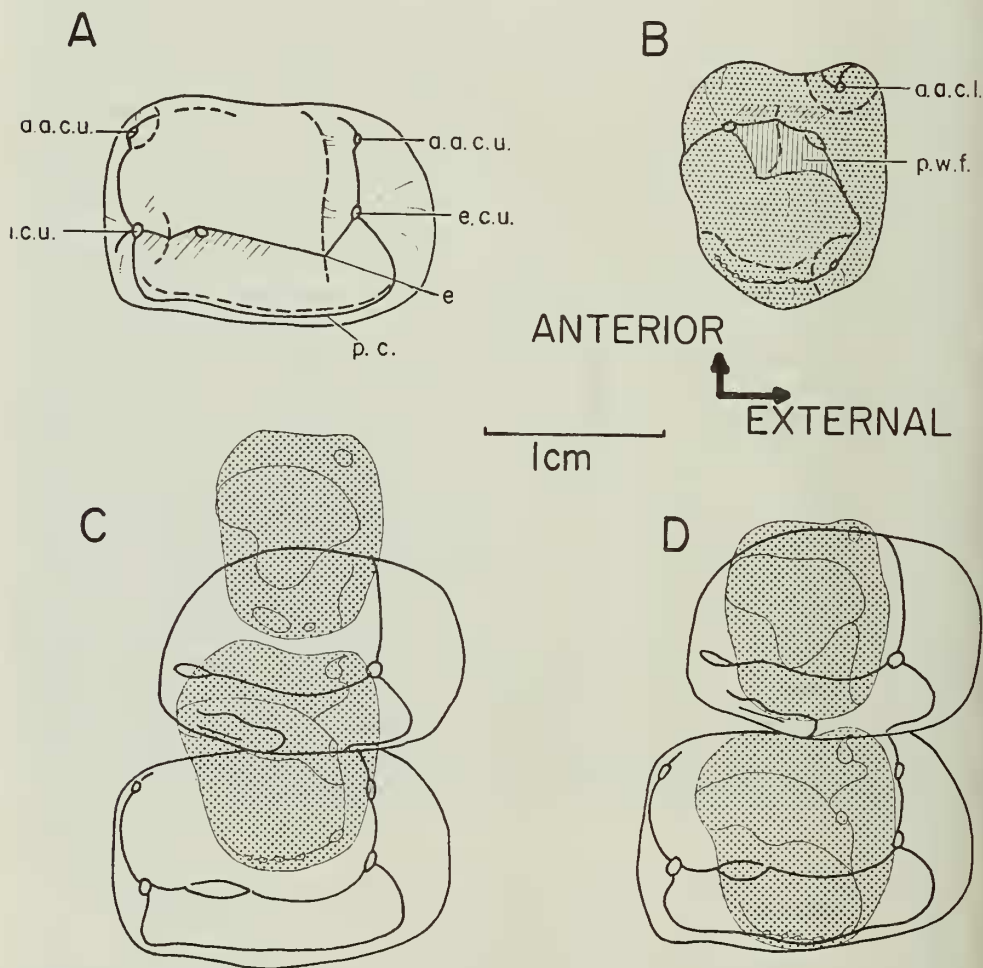


FIG. 7. *Scalenodon hirschsoni* sp. nov. Postcanine teeth. A. Crown view of upper. B. Crown view of lower. C. Crown views of uppers and lowers superimposed to show the relative positions at the beginning of dynamic occlusion. D. The same, at the end of dynamic occlusion.

than the portion behind; this is probably due more to addition to the anterior part of the crown than to a posterior migration of the transverse ridge because small additional cusps (a.a.c.u.) are present on the ridges running forwards from both external and internal main cusps. The embayment between the external and central main cusps (Fig. 8A) is deeper than that of *S. angustifrons* and the transverse ridge is not as high as in the latter species. A fairly prominent posterior cingulum (Fig. 7A, p.c.) is present.

In the lower postcanines (Fig. 7B) the transverse ridge formed by the two main cusps is not as high as that of *S. angustifrons* and the anterior accessory cusp (a.a.c.l.) is larger. Details of occlusion and of the amount of longitudinal movement during mastication are illustrated in Figs 7C-D, 8A-D and 9A-E. Because the transverse ridge of the uppers also is lower than in *S. angustifrons* and because it was apparently worn down fairly rapidly, its posterior surface does not form a high wall (see internal views of beginning and end of dynamic occlusion, Fig. 8C-D); nevertheless small matching wear facets on that surface and on the anterior surface of the transverse ridge of the lower postcanines indicate that some shearing took place in this position. The mandibular movements which probably took place during occlusion have been reconstructed by manipulating the opposing jaws and by studying the striations on the wear facets of opposing teeth. These movements are illustrated in Fig. 9 in external view by showing several positions of the lower postcanines 5 and 6 relative to the upper postcanines 4 and 5. As the jaws closed, the anterior part of the external surface of the main cusps of lowers 5 and 6 sheared past the internal surfaces of the external main cusps of uppers 4 and 5 (Fig. 9A-B). As the mandible proceeded backwards (Fig. 9B-C-D) the external surface of the external main cusp of lower postcanine 5 sheared past the internal surface of the external main cusp of upper postcanine 5. This shear, as it would have appeared in internal view, is illustrated in Fig. 8C-D. The wear facets on the external surface of the lower postcanines resulting from this backward movement are shown in Fig. 9F. The important point is that at the beginning of dynamic occlusion the transverse ridge of the 5th lower postcanine lay behind the transverse ridge of the 4th upper postcanine (Fig. 7C). In essence, therefore, occlusion resulted from a posterior and a vertical jaw movement, just as in *S. angustifrons*. However, a lightly worn 5th lower postcanine of *S. hirschsoni* shows a distinct wear facet (Fig. 7B, p.w.f.) on the *posterior* surface of the main cusp; this matches a wear facet on the *anterior* surface of the transverse ridge of the 5th postcanine. It is difficult to account for these facets if the power stroke of the lower jaw was directed dorso-posteriorly. Admittedly they could have resulted from the postero-dorsal surface of the transverse ridge of the lower tooth being drawn backwards and downwards across the antero-ventral surface of the transverse ridge of the upper. This movement, as it would appear in external view, is shown in Fig. 9D. Although this would have involved crushing between the opposing transverse ridges, it would have required that the lower postcanines be dragged down an inclined plane. The same wear facets, however, would have been formed if the mandible had moved forwards and upwards during dynamic occlusion as shown in Fig. 9E so that the leading edge of the transverse ridge of the lowers sheared past the trailing edge of the transverse ridge of the uppers. This movement

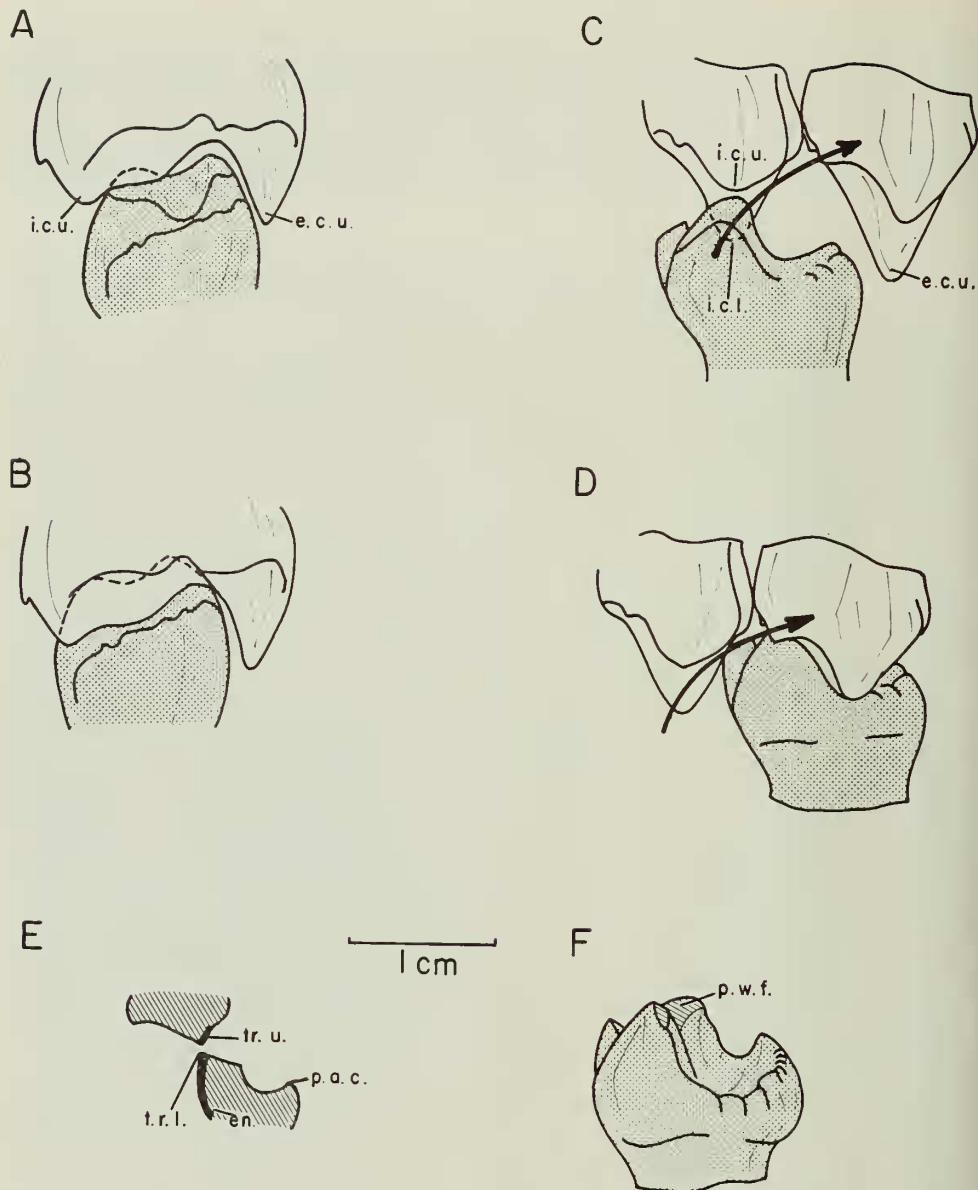


FIG. 8. *Scalenodon hirschsoni* sp. nov. Postcanine teeth. A. Posterior view at the beginning of dynamic occlusion. B. Posterior view at the end of dynamic occlusion. C. Oblique internal view at the beginning of dynamic occlusion. D. Oblique internal view at the end of dynamic occlusion. E. Sagittal section through part of opposing postcanines to show matching shearing surfaces resulting from anteriorly directed power stroke. F. Internal view of lower postcanine to show wear facet resulting from anteriorly directed power stroke.



as it would appear if a longitudinal section were cut through the teeth, is shown in Fig. 8E; the enamel-like material (en.) is considerably thicker on the anterior surface of the transverse ridge of the lower tooth than on the occlusal surface or in the posterior basin, just as would be expected if this species were capable of a forwardly directed power stroke as well as the usual backwardly directed stroke.

#### 4. Postcanine dentition of *Scalenodon attridgei*

This species is known only from an isolated snout, with the upper teeth well preserved on both sides. The postcanine row (Fig. 10A, B, Plate 6) of eight teeth ends behind in three teeth which become progressively smaller, as in many specimens of *S. angustifrons*. The first five teeth are so worn that most of the details of crown structure are lost, but the 6th and 7th postcanines are only slightly worn and the 8th not at all. Although the last two teeth are smaller than the more anterior ones and would presumably have been replaced later in life by larger gomphodont teeth, they are of great interest. The basic pattern of the postcanines of *S. attridgei* is similar to that of *S. angustifrons* and *S. hirschsoni*. They are, however, set obliquely in the maxilla, and the internal surface is slightly wider than the external surface. The

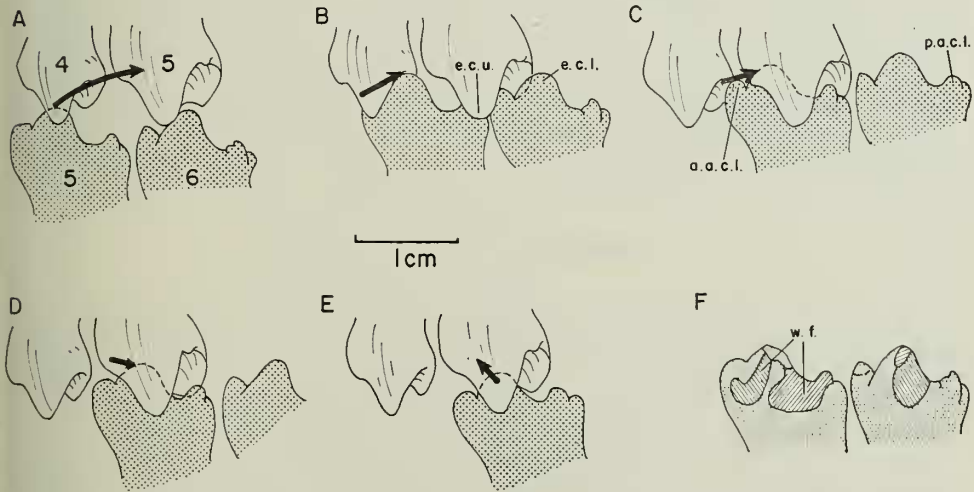


FIG. 9. *Scalenodon hirschsoni* sp. nov. Postcanine teeth. A-D. External views to show successive stages of the posteriorly directed power stroke. Heavy arrow in A indicates total extent of backward movement involved. E. D. The same, but to show anteriorly directed power stroke. F. External view of lower teeth to show wear facets on the external surfaces.

important feature of the upper postcanines of *S. attridgei* is the presence of a row of well developed cuspules along the anterior border of the crown of postcanines 7 and 8; in postcanines 5 and 6 they have been obliterated by wear. The antero-medial cuspule (a.a.c.u.) is the largest of these cuspules and they tend to become smaller towards the exterior (Fig. 10B). A high ridge joins the external main cusps to the most external cuspule of the anterior row. The central and internal main cusps (c.c.u. and i.c.u.) are both large and well differentiated and form the transverse ridge. A basin (b.u.) is present in the occlusal surface of the crown; this is bordered behind by the transverse ridge, in front by the anterior row of cuspules and externally by the vertical inner wall of the external main cusp. A deep valley separates the internal main cusp and the most internal cuspule of the anterior row (a.a.c.u.) so that the basin is completely surrounded except for this narrow valley opening internally. In the 7th postcanine the tips of the central and internal main cusps and the tips of the cuspule forming the anterior ridge are worn away. In the more anterior teeth wear has tended to obliterate the original details of the crown pattern and especially the anterior row of cuspules. The tips of the central and internal main cusps and the crest of the transverse ridge have been worn away so that the occlusal surface of the crown in front of the transverse ridge is a plane sloping slightly upwards in an antero-external direction; this is best seen in the anterior view of the upper postcanines (Fig. 10B). Except for two internal cuspules, most of the cuspules of the anterior row of the 6th postcanine have been worn away and only a low wall remains. A feature of the crown of the 5th and 6th postcanines which is not present in the smaller 7th and 8th is a faint posterior ridge or cingulum (p.c.) close to the posterior margin of the crown. A shallow valley which widens slightly towards the external side lies anterior to it; this will be referred to as the posterior basin (p.b.). The wide forward and upward sloping flat surfaces of the crowns of the upper postcanines of *S. attridgei* could have resulted from both antero-dorsal and postero-dorsal power strokes. The postcanines of the Brazilian species *Traversodon stahleckeri* (von Huene 1944 : 48) are extremely worn, but from what remains of the upper teeth they appear to have been similar to those of *S. attridgei*.

#### 5. Postcanine dentition of *Scalenodon charigi*

This specimen, consisting of an isolated maxilla with two posterior postcanines, was previously compared (Crompton, 1955) with the Brazilian species *Gomphodontosuchus brasiliensis*. Although the teeth were badly damaged several details can still be seen, and, now that more traversodontids from South America and East Africa have been described and figured, additional comments may be made.

The teeth (Fig. 10C) are set obliquely in the maxilla. The external anterior accessory cuspule (a.a.c.u.) is larger than in *S. hirschsoni* and the internal surfaces of the two external cusps form a high shearing surface. The main transverse ridge is situated near the posterior edge of the crown. The central cusp appears to be absent. The anterior wall is high and is terminated internally by a high rounded cuspule (a.a.c.u.); consequently the anterior basin (b.u.) is deep and occupies most of the occlusal surface of the crown. The shearing surface on the internal face of the



external cusp is continuous with that on the posterior surface of the anterior wall of the same tooth; this suggests that the anterior surface of the transverse ridge of the corresponding lower postcanine sheared up the anterior wall of the upper postcanine rather than across it. Although the anterior wall was present in *S. attridgei*, it was

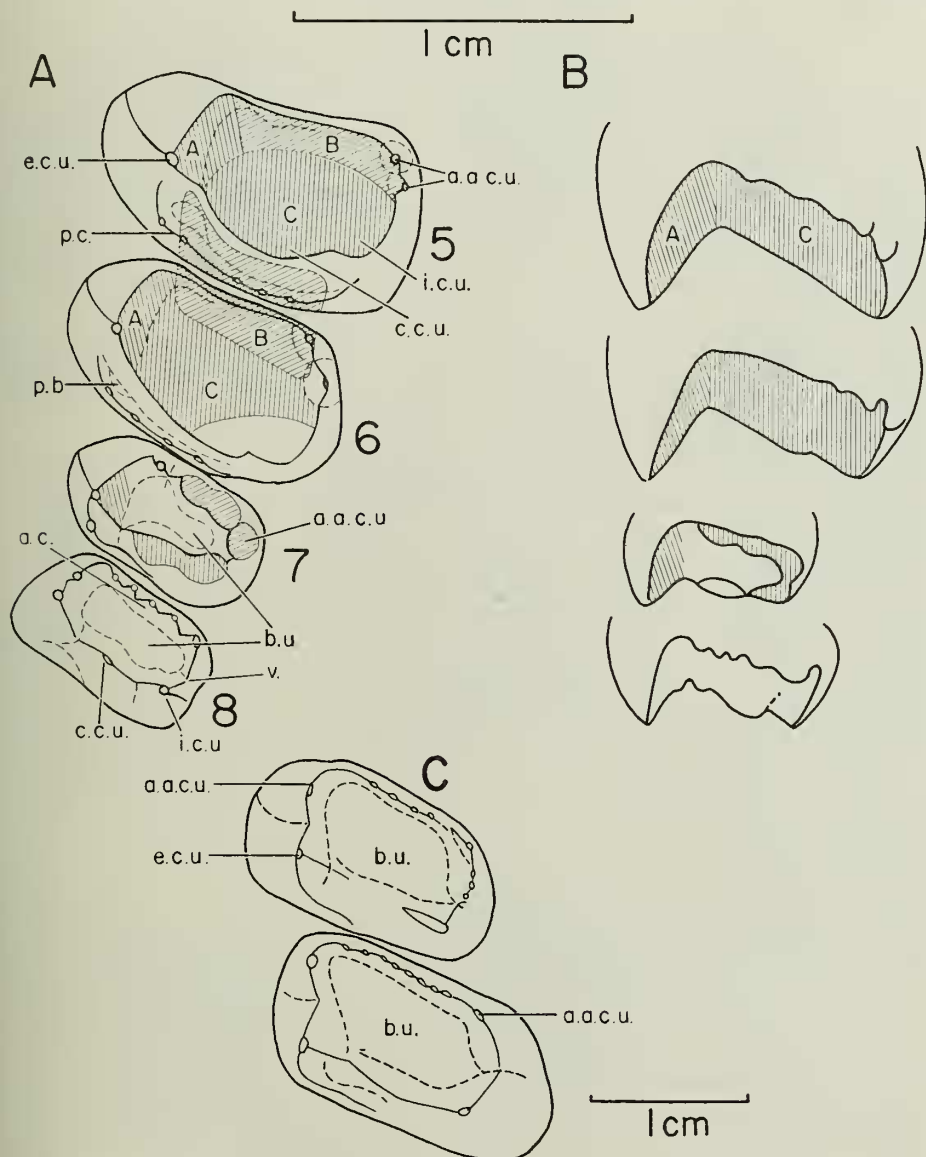


FIG. 10. A. *Scalenodon attridgei* sp. nov. Crown view of last four upper postcanines. B. *Scalenodon attridgei* sp. nov. Anterior views of the same. C. *Scalenodon charigi* sp. nov. Crown view of last two upper postcanines. For key to abbreviations see p. 69.

rapidly worn away and apparently did not form a significant vertical shearing surface. The structure of the anterior wall, the absence of a central cusp and the oblique position of the crown relative to the longitudinal axis of the palate are reminiscent of the South American genus *Exaeretodon*.

#### 6. Occlusion and jaw movements in a species of *Massetognathus*

The postcanines of the Argentine traversodontid *Massetognathus pascuali* have been described in detail by Romer (1967), but he does not discuss occlusion in detail. Dr. Bonaparte presented the Peabody Museum with a jaw fragment that has been tentatively assigned to the genus *Massetognathus*, and in which upper and lower postcanines were preserved in tight occlusion; the jaws have been carefully separated by Mr C. Schaff. Distinct wear facets are preserved on most of the teeth, and by matching upper and lower wear facets it has been possible to determine the jaw movements that must have taken place in *Massetognathus* during the final stages of the masticatory cycle. Although the postcanines are almost identical to those of *M. pascuali* the wear pattern is slightly different and the fragment should perhaps be placed in a different species or genus. This may be possible when the entire fauna of gomphodont cynodonts from Chañares is fully described.

The postcanines (Fig. 11 & Plate 7) are very similar to those of *S. angustifrons* except that two accessory cuspules rather than one are present on the ridge leading forwards from the external main cusp, which latter lies further back than in *S. angustifrons*. A characteristic feature of *Massetognathus* and *Exaeretodon* not present in the African traversodontids is that the external margin of the upper postcanines as seen in crown view is drawn outwards and backwards (Fig. 11B) to form a distinct lobe. The transverse ridge is high and forms the posterior border of the crown, the posterior cingulum being but poorly developed. The inner surface of the external main cusp and of the two anterior accessory cuspules forms a high vertical wall which is more pronounced than in *S. angustifrons*. The point of junction between the transverse ridge and the external main cusp lies near the posterior border of the crown. The lower postcanines are similar in structure to those of *S. hirschsoni* but lack the anterior accessory cuspules. As in all gomphodont cynodonts the amount of wear increases progressively towards the front of the jaw. Matching shearing planes are shown in Fig. 11D & E. As the teeth came into occlusion the outer surface of the 4th lower postcanine (Fig. 11D) sheared past the internal surface of the external main cusp of the 3rd upper postcanine (wear facets 2 in Fig. 11C, D & E); then, as the jaws continued to close, it also sheared past the inner surface of the two anterior accessory cuspules of the 4th upper postcanine (wear facets 1). The two facets, 2 and 1, on the 3rd and 4th upper postcanines respectively, are therefore continuous. This action was similar to that in *Scalenodon*. At the beginning of occlusion the tips of the two main cusps of the 4th lower postcanine lay anterior to the tips of the central and external main cusps of the 3rd upper postcanine, i.e. the transverse ridge of the lower lay in front of the transverse ridge of the upper (Fig. 14). The central cusp of the upper lay directly behind the valley separating the two lower cusps. Because of this, as the mandible was drawn back-

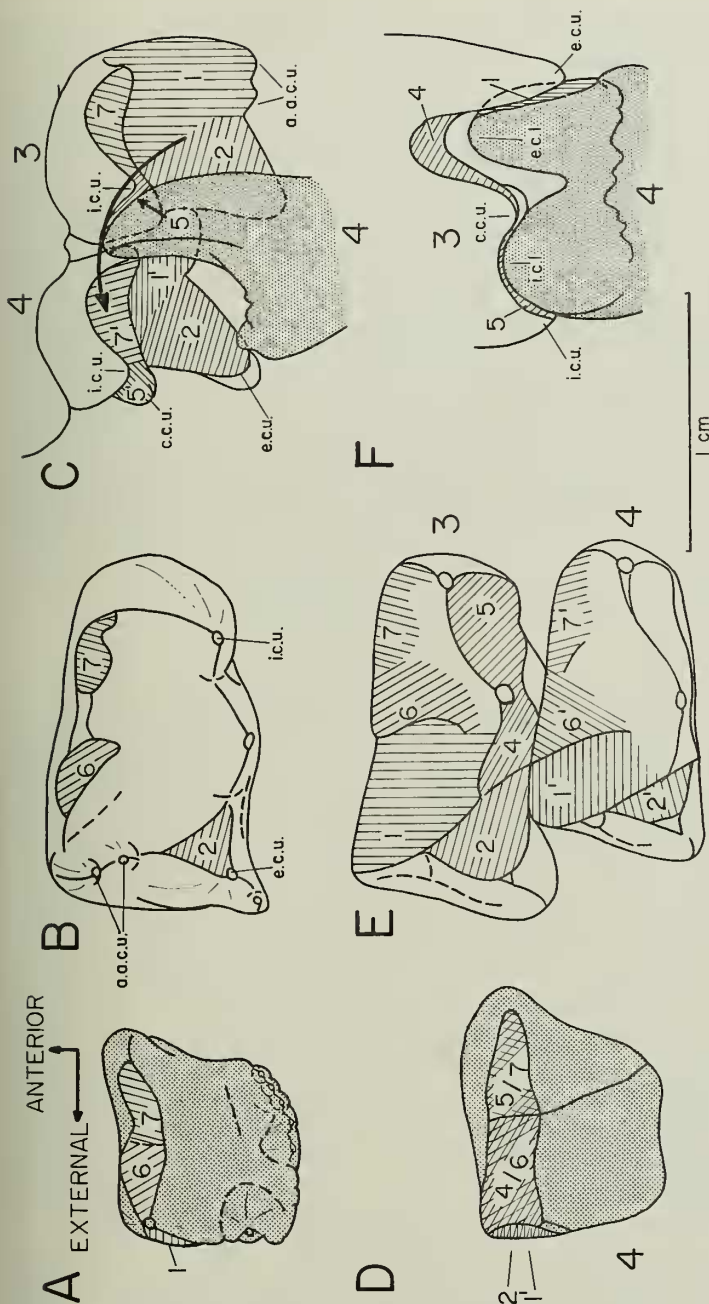


FIG. 11. *Massetognathus* sp. (specimen in Yale Peabody Museum). Postcanine teeth. A. Crown view of slightly worn lower. B. Crown view of slightly worn upper. C. Internal view to show the depth of the shearing surfaces on the internal faces of the external cusps of the upper teeth and the movement (heavy arrow) of a lower tooth relative to the uppers during the final stages of the power stroke. D. Crown view of lower. E. Crown view of two uppers } to show matching shearing surfaces. F. Posterior view of opposing pair at the beginning of dynamic occlusion.

wards and the lower cusps were dragged across the transverse ridge, pronounced wear facets were formed on either side of the central cusp of the uppers and on the tips of the main cusps of the lowers. These matching facets have been numbered 4 and 5 in both uppers and lowers (Fig. 11, D & E). As the mandible was drawn further back the main cusps of each lower tooth carved grooves into the anterior wall of the succeeding upper tooth. These grooves have been numbered 6<sup>1</sup> and 7<sup>1</sup> on the upper tooth (Fig. 11E) and the matching shearing surfaces 6 and 7 on the lower tooth (Fig. 11D). It is clear from the orientation of these matching facets that they were produced by the backward and upward movement of the mandible during the final stages of the masticatory cycle. A study of the wear facets in this species of *Massetognathus* therefore suggests that, as in *S. angustifrons*, the jaws were drawn backwards during dynamic occlusion; but those facets which suggest an anteriorly directed power stroke in *S. hirschsoni* and *S. attridgei* are absent in *Massetognathus*. Perhaps the most important feature of occlusion in this species of *Massetognathus* is that the transverse ridge of the lowers was drawn across the transverse ridge of the uppers. This was not the case in *Massetognathus pascuali*, *S. angustifrons* or *S. hirschsoni*, where the anterior surface of the transverse ridge of the lowers sheared up the posterior surface of the transverse ridge of the uppers. It is possible to derive the situation in the new species of *Massetognathus* from that in *S. angustifrons* simply by increasing the extent of the antero-posterior movement during occlusion. This is important when considering the ancestry of the tritylodontids.

#### 7. Postcanines of *Exaeretodon* and *Gomphodontosuchus*

Bonaparte (1962) has described the teeth of *Exaeretodon frenguelli*; I was able to study postcanine teeth of this species in the Museum of Comparative Zoology at Harvard and at the Instituto Miguel Lillo in Tucumán. The upper postcanines (Fig. 12A, B, C) are similar to those of *Massetognathus*; and the postero-external extension of the external region is so marked that the tooth as seen in crown view may be divided into two lobes, a lateral and a medial. Well developed external (e.c.u.), anterior accessory (a.a.c.u.) and posterior accessory (p.a.c.) cusps are present on the external margin of the tooth; their internal surfaces form a continuous antero-posteriorly aligned shearing surface which extends right along the tooth from front to back. The transverse ridge terminates short of the base of the external main cusp; its central cusp is absent. Two anterior accessory cusps (a.a.c.u.) are present, one internal and one external. In posterior view (Fig. 12C) it can be seen that the crest of the transverse ridge rises very sharply ventrally towards the tip of the internal main cusp. The anterior wall (a.w.) of *Exaeretodon* is a prominent feature; it can be seen in anterior view (Fig. 12B) that it too rises very sharply ventrally to terminate in the internal anterior accessory cusp. A shallow basin separates this anterior wall from the transverse ridge. The cutting surface on the inner face of the external main cusp of each tooth is continuous with those in front and behind.

Because the anterior wall and the transverse ridge of each upper postcanine lie obliquely the internal main cusp of each lower postcanine is considerably further back than the external (Fig. 12D). Mandibular movements during dynamic



occlusion were probably similar to those of *Massetognathus pascuali* and *Scalenodon angustifrons*. Wear facets indicate that the transverse ridges of the upper and lower postcanines were not drawn across one another from front to back but it appears that, instead, the primitive transverse shear still took place between the anterior surface of the transverse ridge of the lower tooth and the posterior surface of the transverse ridge of the upper. There is no indication that there was a forwardly directed power stroke. However it will not be possible to discuss jaw movements in *Exaeretodon* with any degree of confidence until the wear facets on the abundant postcanines have been studied.

The lower postcanines of the southern African traversodontid *Scalenodontoides macrodentes* Crompton & Ellenberger 1957 are almost identical in size and structure with those of *Exaeretodon*. *Scalenodontoides* was found in association with melanorosauroid (prosauropod) dinosaurs and is therefore younger than the East African traversodontids.

I have been unable to study the type of *Gomphodontosuchus brasiliensis* (von Huene 1944-48) and the following remarks are based upon stereophotographs of the specimen taken by Dr J. Hopson. This genus has exaggerated some of the features of the postcanines of *Exaeretodon*. The teeth are set in the jaw more

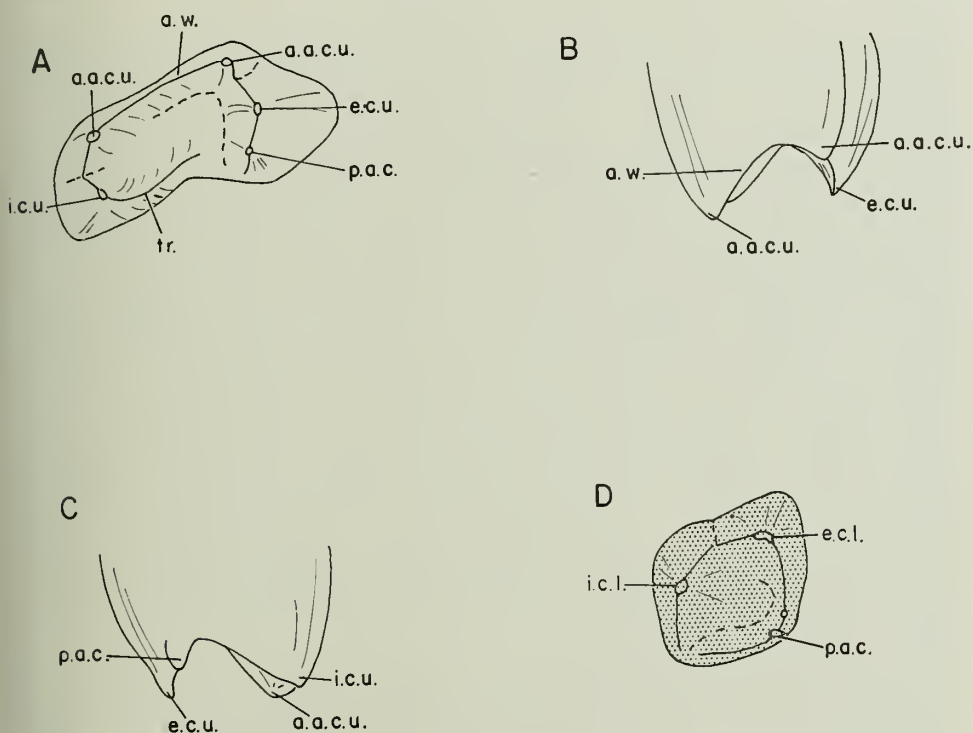


FIG. 12. *Exaeretodon frenguelli*. Typical postcanine teeth. A. Crown view of upper. B. Anterior view of upper. C. Posterior view of upper. D. Crown view of lower. For key to abbreviations see p. 69.



obliquely so that the angle between the transverse ridge and the inner shearing surface of the external cusp is smaller than in *Exaeretodon*; the obliquity is reflected also in the outline of the crowns of the lower postcanines. In *Gomphodontosuchus* the anterior wall of the upper postcanine is higher than in *Exaeretodon*, the crown basin therefore deeper; this presumably indicates an increase in the cutting function of the anterior wall.

#### V. DISTRIBUTION OF THE TRAVERSODONTIDAE

Traversodontids are known to have existed for a long period of time and their dentitions indicate that they occupied several different ecological niches. At present they are known with certainty only from Africa and South America; indeed, this is true of all gomphodont cynodonts, and it has therefore been suggested that they were restricted to the southern continents. However, a large lower jaw of what may prove to be traversodontid cynodont was discovered in the Upper Triassic Wolfville Formation of the Newark Group in Nova Scotia by Dr R. L. Carroll and Dr D. Baird (Romer, 1967); unfortunately no postcanine teeth were preserved *in situ*, but the size of the jaw and the structure of the symphysis showed close similarity to *Scalenodontoides macrodentes* from southern Africa.

The postcanine teeth of traversodontids from several horizons and numerous localities in Africa are remarkably similar to those of traversodontids from various localities in South America. *Scalenodon angustifrons* closely resembles *Massetognathus pascuali*; *S. charigi* closely resembles *Exaeretodon frenguelli* and *Gomphodontosuchus brasiliensis*; and *S. attridgei* closely resembles *Traversodon stahleckeri*. The traversodontids of the Chañares Formation (*Massetognathus*) are comparable in size to the various species of the East African *Scalenodon*, but, while no East African form approaches the gigantic size of the traversodontids from Ischigualasto (*Exaeretodon*, *Proxaeretodon* and *Ischignathus*), *Scalenodontoides* from southern Africa indicates that large gomphodont cynodonts were present on that continent during Late Triassic times. Unfortunately the traversodontids collected in Brazil (Colbert, 1963) have not yet been described. No African site has been discovered which has yielded traversodontids in anything like the abundance of those of South America.

The similarity of the terrestrial Early Triassic faunas from Argentina recently described by Bonaparte (1967b) and of terrestrial Middle Triassic faunas from various parts of South America to African faunas of corresponding age, including the cynodonts, may indicate a close connection—or at least easy migration routes—between Africa and South America during Triassic times. Recent views (Bullard 1969, Menard 1969) on the relative positions of the continental masses of Africa and South America before the end of the Cretaceous suggest that they were extremely close, if not united, during the Trias.

Early cynodonts (Late Permian to Early Triassic) are known from South America (Bonaparte, 1967a), South Africa (Haughton & Brink, 1954), East Africa (Parrington, 1936), China (Young, 1961), and Russia (Tatarinov, 1968). A carnivorous cynodont of Early to Middle Triassic age probably occurs in China (Young, 1959). The descendants of the cynodonts, the tritylodontids, have been discovered in Late Triassic de-

posits in South America (Sill, 1969), Africa (Fourie, 1968), China (Young, 1947), North America (Colbert, *pers. comm.*) and Europe (Kermack, 1965 and Kühne, 1956). Early mammals, also the descendants of cynodonts, have been discovered in the Late Triassic of southern Africa (Crompton, 1964), China (Rigney, 1963) and Europe (Kermack, 1965). In view of the world-wide distribution of these related groups it would not be expected that cynodonts should be totally absent from northern continents during Middle Triassic times. In particular, the gomphodont cynodonts may therefore have enjoyed a world-wide distribution; it may just be that their northern representatives (other than the jaw found by Carroll and Baird in Nova Scotia) have not been discovered as yet, and their apparent absence from northern continents may be due to the lack of suitable continental deposits of Middle Triassic age rather than to the absence of the animals themselves (Colbert, 1963).

The distribution of other Middle Triassic groups tends to support this view. For example, several Middle Triassic archosaurs are known from southern continents (Charig, 1967), but only a few, almost accidental finds are all that is known of the archosaurs of this age from northern continents (Krebs, 1965).

#### VI. OCCLUSION IN *TRITYLODON* AND THE ORIGIN OF THE TRITYLODONTIDAE

Several features of the skull and dentition of the traversodontids suggest that a member of this family may have been ancestral to the tritylodontids. This suggestion, made originally by Crompton & Ellenberger in 1957, is supported by the new material. The crowns of the upper cheek teeth of *Tritylodon* (Fig. 13J) consist essentially of three longitudinal rows of crescent-shaped cusps, three cusps each in the internal and central rows and two cusps in the external row. The corresponding lowers (Fig. 13K) consist of two rows each of three crescent-shaped cusps. The crescent of the upper cusps are concave forwards, whereas the crescents of the lower cusps are concave backwards (Fig. 13L). The two rows of lower cusps occluded between the three rows of upper cusps. Wear facets bearing parallel striations are developed on both surfaces of all the cusps except the outer surface of the external cusps of the uppers and the inner surface of the internal cusps of the uppers, which do not face any other surface; they indicate that during mastication the jaws moved horizontally. The extent of movement during occlusion is shown in Figs 13L and 14. The lower postcanine commenced dynamic occlusion by making contact with the upper tooth one position further forward in the upper jaw. The anterior edges of the upper cusps and the posterior edges of the lower cusps formed a multiple cutting mechanism which would have been effective only if the power stroke during mastication were directed backwards. Occlusion therefore involved the dragging of the tips of the central row of cusps of the upper teeth and of the tips of both rows of cusps of the lowers across the floors of the valleys between the longitudinal rows of cusps of the opposing teeth. As a result these crescentic cusps were rapidly worn down, thereby decreasing the shearing action of their near-vertical surfaces. In many specimens of tritylodontids the crowns of the postcanine teeth consist of almost flat surfaces scarred by longitudinal grooves. The backward jaw movements during occlusion, the rapid wearing down of teeth, the eruption of new teeth at the back to provide

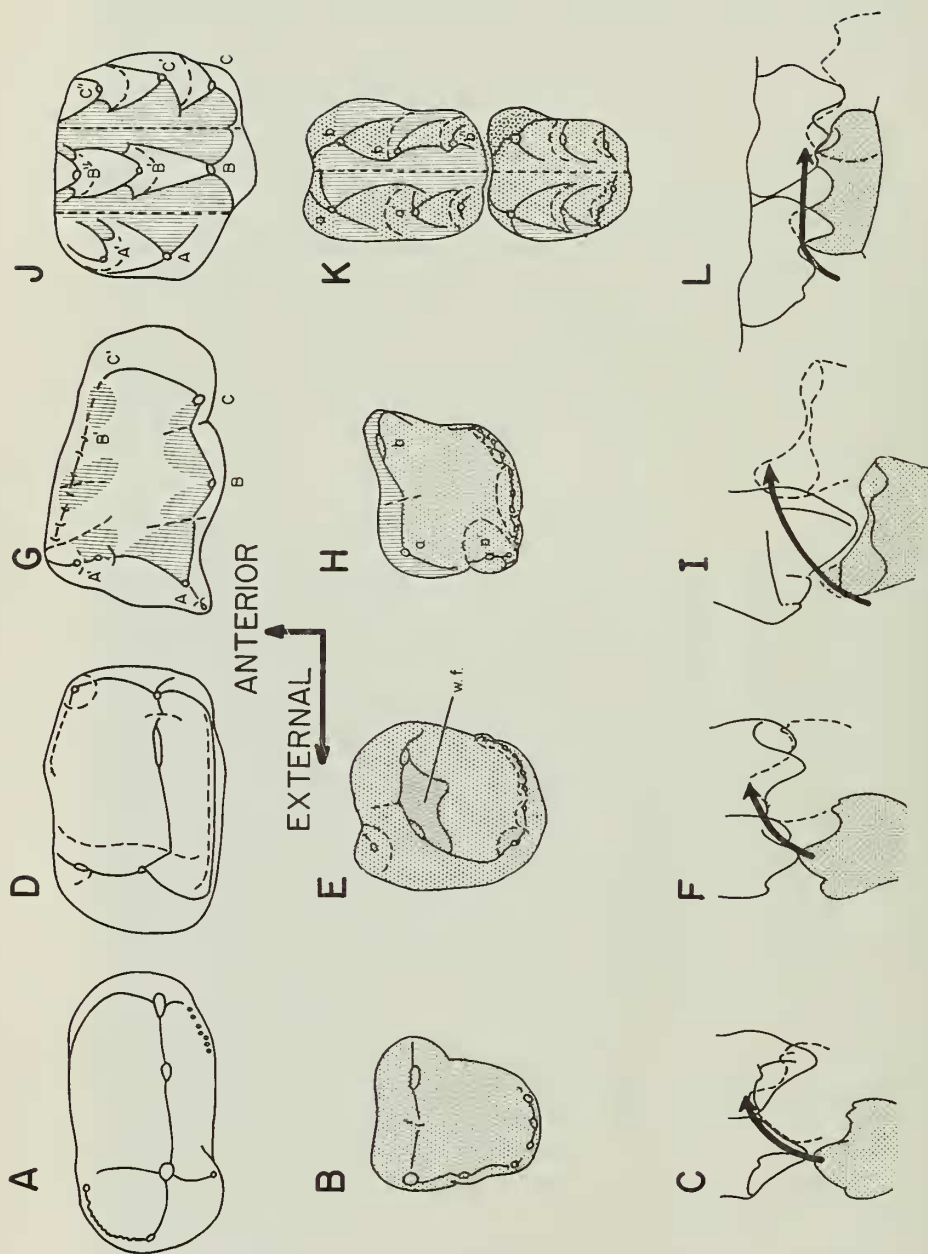


FIG. 13. *Scalenodon angustifrons*. Postcanine teeth. A. Crown view of upper. B. Crown view of lower. C. Lateral view of final stages of dynamic occlusion. *Scalenodon hirschi* sp. nov. Postcanine teeth. D. Crown view of upper. E. Crown view of lower. F. Lateral view of final stages of dynamic occlusion. *Mastognathus* sp. (specimen in Yale Peabody Museum). Postcanine teeth. G. Crown view of upper. H. Crown view of lower. I. Lateral view of final stages of dynamic occlusion. *Tritylodon* sp. Postcanine teeth. J. Crown view of upper. K. Crown view of lower. L. Lateral view of final stages of dynamic occlusion.

new shearing surfaces and the loss of worn teeth in front, as well as numerous skull and skeletal features, suggest a close relationship between the tritylodontids and traversodontids. In addition there are several other similarities between the dentitions of individual traversodontids and of *Tritylodon*. These are most marked in *Scalenodon hirschsoni* and the new species of *Massetognathus* described above. In *Tritylodon* and *S. hirschsoni* the rows of postcanine teeth are parallel to the longitudinal axis of the skull and are not arranged obliquely along the edge of the maxilla as in *S. attridgei*, *S. charigi* and earlier cynodonts. The incisors and lower canines of *S. hirschsoni* are procumbent and this, taken together with the parallel postcanine rows, may indicate that there was increased posterior jaw movement during mastication. In *Massetognathus* the postcanine rows are not parallel but there is nevertheless a marked tendency for the rows to be directed away from the edge of the face towards the midline of the skull (Romer, 1967). The nature of the shearing planes between the external surface of the lower postcanines and the internal surface of the external cusps of the upper postcanines was essentially the same in *Tritylodon* and the two traversodontid genera (cf. Fig. 13C, F, I & L). In both *Tritylodon* and the traversodontids lower postcanines occluded with two upper postcanines because of the extensive backward movement of the lower jaw during occlusion. The main difference lies in the presence of the additional cusps of the postcanines in *Tritylodon*. However, cusps that were not present in the more primitive traversodontid *S. angustifrons* (Fig. 13A) were added to the crown of *S. hirschsoni* (13D) and *Massetognathus* (13G).

In these latter animals cusps have been added to the uppers in front of the external and internal main cusps, i.e. in positions which suggest the initial steps in the formation of the external and internal rows of cusps of the tritylodontid upper postcanines. It is significant that the largest cusps of tritylodontid upper postcanines are situated posteriorly and that the anterior cusps decrease progressively in size. The posterior accessory cusps on the external surface of the lower postcanines of traversodontids may also indicate the initial step in the greater development of the external row of cusps typical of tritylodontid lower postcanines. Although the postcanines of *S. hirschsoni* tended to resemble those of tritylodontids it is unlikely that the former reptile was ancestral to the latter; the power stroke was directed forwards in *S. hirschsoni*, whereas it is the backwardly directed power stroke which appears to have characterized *Tritylodon* occlusion. In *Tritylodon* the external and internal rows of cusps of the lower postcanines sheared between the external, central and internal cusps of the corresponding upper postcanines; therefore, if the ancestor of *Tritylodon* were to be found amongst the traversodontids, some indication of this occlusal pattern would be expected in one of the latter. In all the species of *Scalenodon* the transverse ridge of each lower tooth always occluded with the posterior surface of the transverse ridge of the preceding upper tooth; this shows that the lower jaw was not thrust far enough forwards before the power stroke for the transverse ridge of the lowers to be drawn backwards over the transverse ridge of the uppers. In the new species of *Massetognathus* however, the transverse ridges were drawn across one another during occlusion; this appears to be the only known traversodontid where this happened. Neither this species of *Massetognathus* nor *S. hirschsoni* appears to



be directly ancestral to the tritylodontids, but, taken together, they show that some traversodontids were developing a postcanine dentition and mandibular movements which were very close to those of tritylodontids. Once two transverse ridges shearing past one another had been developed, it was a relatively simple matter to add more cusps in front of the uppers and behind the lowers, and thus to obtain postcanines of the tritylodontid type. In Fig. 13G & J an attempt has been made to homologise the cusps and regions of the crowns of the upper postcanines of the new species of *Massetognathus* and of *Tritylodon*. The posterior transverse row of cusps has been labelled A, B and C; the second row A<sup>1</sup>, B<sup>1</sup> and C<sup>1</sup> and the third row B'' and C''. In Fig. 13H & K the same has been attempted for the lower teeth. It is clear that forms such as *Exaeretodon*, *Gomphodontosuchus* and *S. charigi*, which had lost the central cusp of the upper postcanines, could not have been ancestral to the tritylodontids; neither could forms such as *S. attridgei* with strongly developed anterior masticatory movements.

#### VII. SUMMARY AND DISCUSSION

The postcanine teeth of all the major groups of cynodonts have been briefly described and figured.

Three new species of traversodontid cynodonts, *Scalenodon hirschsoni*, *S. attridgei* and *S. charigi* have been named and briefly described from their postcanine teeth.

An attempt has been made to trace the evolution of postcanine occlusion in advanced cynodonts. This is shown diagrammatically in Fig. 14. The term occlusion implies that there was tooth-to-tooth contact during the masticatory cycle; the teeth were constructed so that shearing, puncturing and crushing were possible between corresponding upper and lower teeth. Occlusal relationships

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FIG. 14. Origin of the postcanines of *Tritylodon*. For each species the superimposed crown views of upper and lower postcanines are shown next to a posterior view of an occluding pair. Heavy lines indicate the orientation of the shearing planes. White circles indicate the principal cusps of the upper postcanines and black circles the principal cusps of the lower postcanines. Arrows indicate the extent of backward movement, from the beginning of tooth contact to its tightly closed completion. A. *Thrinaxodon* sp. Tooth-to-tooth contact did not occur. B. *Trirachodon* sp. C. *Diademodon* sp. Lowers occluded directly with uppers and small shearing surfaces were produced by wear. D. *Scalenodon angustifrons*. Crowns of uppers and lowers were modified to reduce destruction of the tips of the cusps, and transverse elongated shearing surfaces were present. These surfaces came into use as the lower jaw was drawn upwards and backwards. G. *Exaeretodon* sp. A modification of the *S. angustifrons* pattern. H. *Scalenodon hirschsoni* sp. nov. Occlusion involved both an anteriorly directed power stroke and a backwardly directed one. E. *Massetognathus* sp. The transverse shearing surface of the lower postcanines was drawn across the transverse shearing surface of the corresponding uppers (this did not happen in D, G & H above); the transverse shearing surfaces were modified in that small longitudinal shearing surfaces were formed by wear. F. *Tritylodon* sp. The addition of extra cusps, in front of the upper teeth and behind the lowers, increased the length of the longitudinal shearing surfaces (which were comparable to those formed by wear in *Massetognathus*). There were no transverse shearing surfaces. The series from *Diademodon* to *Tritylodon* shows a progressive increase in the extent of the backward movement of the lower jaw during the power stroke.



become progressively more complex within the cynodonts.

In the early cynodonts, the Galesauridae and Procynosuchidae, the lower postcanines bit internal to the uppers, tooth-to-tooth contact between opposing postcanine teeth was not possible and matching shearing planes are therefore absent (Fig. 14A). In both these families replacement of the postcanine teeth was alternate.

In the carnivorous cynodonts, the Cynognathidae and Chiniquodontidae, the lower postcanines still bit internal to the uppers, but matching shearing surfaces are occasionally found on the external surface of the lowers and internal surface of the uppers; this suggests that some form of shearing was possible, but the shearing

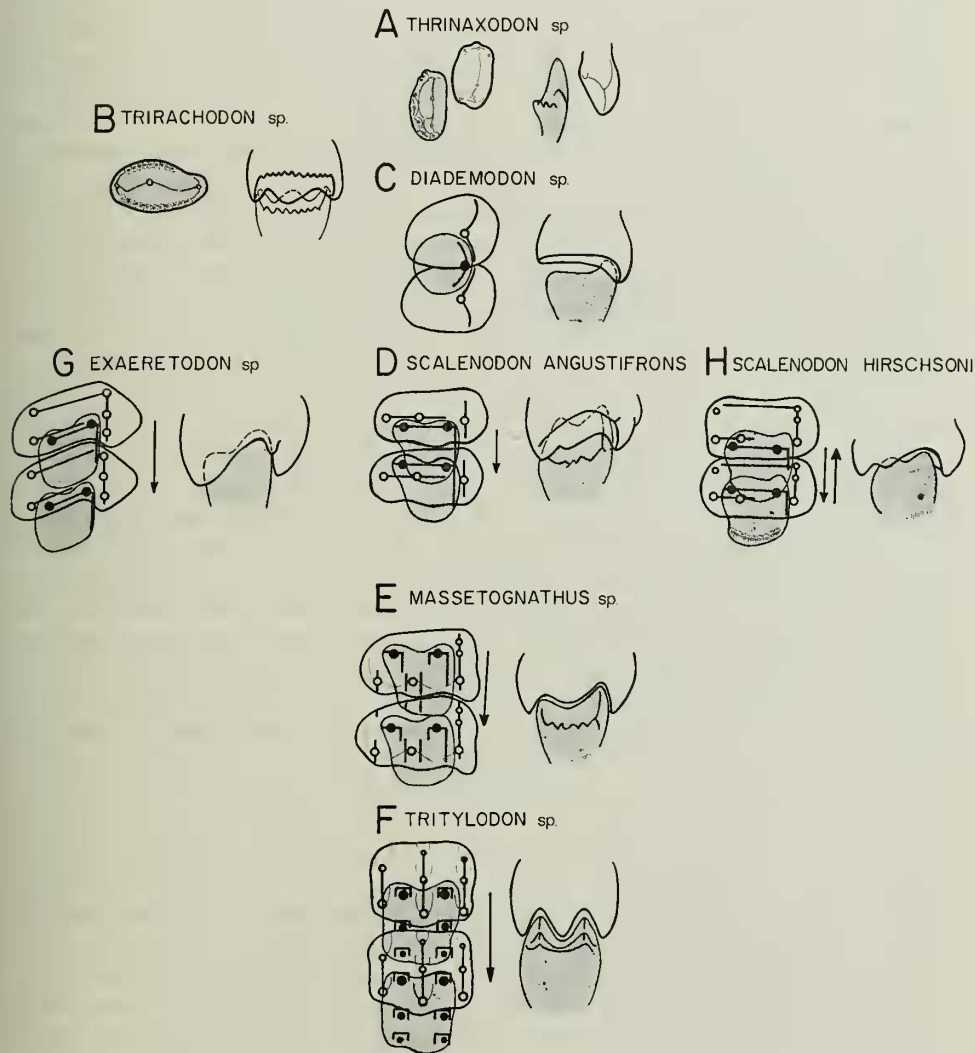


FIG. 14

mechanism was primitive in comparison with mammalian carnassials and presumably played only a minor role in mastication. Clear-cut alternate replacement of the postcanine teeth was lost.

In the gomphodont cynodonts (Diademodontidae, Trirachodontidae and Traversodontidae) the lower postcanine teeth bit directly against the upper postcanines rather than internal to them. In the Trirachodontidae (Fig. 14B) the transverse ridges of the upper and lower postcanines alternated with one another but complex occlusal patterns were not developed. The crowns of the unworn postcanines of the Diademodontidae were characterized by one or two major cusps and an intricate pattern of smaller cusps and ridges; these were rapidly obliterated by wear so that small matching shearing planes were produced on the outer surface of the main cusp of the lower teeth and the inner surfaces of the main cusp of the uppers (Fig. 14C). However, the main cusp of the lower tooth, because it bit directly against the occlusal surface of the uppers (Fig. 14C), was rapidly worn down; the shearing surfaces can have been effective only for a short time. The continued possession of teeth with vertical shearing surfaces was nevertheless ensured by the addition of new gomphodont and sectorial teeth behind, worn teeth being lost from the front of the postcanine row. As would be expected, there was no alternate tooth replacement; occluding teeth were added sequentially at the end of the row during growth.

The occlusal patterns characterizing the Diademodontidae and closely related forms were refined in the Traversodontidae, where high ridges and deep basins provided effective shearing surfaces. Because the tips of the cusps occluded either opposite basins or externally to matching teeth, they were not worn down as rapidly as in the Diademodontidae. In primitive traversodontids the postcanines did not erupt with accurately matching upper and lower shearing surfaces, but, unlike the teeth of Diademodontidae, they needed relatively little wear of the crown surface to produce them; in *Scalenodon angustifrons* these shearing surfaces were aligned both transversely and longitudinally (Fig. 14D). In order that both these planes could be used effectively during the power stroke of mastication, jaw movements during this phase must have been both upwards and backwards. The transverse ridge which connected the two main cusps of the lower postcanine sheared past the transverse ridge formed by the central and internal cusps of the upper postcanine. The backwardly directed power stroke ended when the transverse ridge of the lower postcanine abutted against the anterior surface of the transverse ridge of the following upper. The arrow in Fig. 14D indicates the extent of this backward movement of a lower postcanine relative to the matching upper postcanine teeth during the power stroke of occlusion.

In a specimen belonging to a new species of *Massetognathus* (Fig. 14E) the basic *Scalenodon* type of postcanine was slightly modified. External cusps were added in front of the external main cusp of the upper postcanines and the longitudinal shearing plane was consequently increased in length. This was apparently coupled with an increase in the length of the backwardly directed component of the power stroke. The two main cusps of the lowers commenced shearing in front of, rather than behind, the transverse ridge of the uppers. As the lower jaw was drawn backwards the lower cusps wore grooves between the internal and central cusps and between the

central and external cusps of the uppers; these continued on to the anterior wall of the succeeding upper postcanine. Consequently in the new species of *Massetognathus* what corresponded to the transverse shearing surface of *Scalenodon angustifrons* was broken down into longitudinally orientated shearing surfaces on the sides of the main cusps. As in *Diademodon*, these grooves or shearing surfaces were produced by wearing away a substantial portion of the crown.

In *Tritylodon* (Fig. 14F) these modifications observed in the postcanines of the new species of *Massetognathus* were taken a stage further. The length of the backwardly directed component of the power stroke was increased and cusps were added in front of the upper teeth and behind the lowers. These additional cusps were smaller than the main cusps and they formed two additional transverse rows. Longitudinally orientated shearing planes similar to those which resulted from wear in the new species of *Massetognathus* were present on freshly erupted hardly worn teeth in *Tritylodon*. In *Oligokyphus* an additional row of cusps was added, increasing the length of longitudinally orientated shearing surfaces still further. The entire trend is towards a lengthening of the backward component of the power stroke.

The large South American traversodontids, *Exaeretodon* (Fig. 14G), *Proexaeretodon* and *Ischnathus*, increased the length and height of the vertical shearing surfaces on the internal surfaces of the external main cusps of the upper teeth. The transverse shearing surfaces are obliquely orientated, the central cusp has been lost and a large external cusp added in front of the external main cusp of the uppers. For these reasons it is unlikely that these traversodontids could have been ancestral to the tritylodontids.

In *Scalenodon hirschsoni* (Fig. 14H) and *S. attridgei* wear facets indicate that both longitudinally and transversely orientated shearing planes were present, but, unlike other traversodontids, they could make both forwardly and backwardly directed power strokes during mastication.

The postcanine teeth of traversodontids and the tribosphenic molars of primitive mammals functioned in similar ways. Both have shearing surfaces on the vertical faces of the main cusps and both had jaw movements during the final stages of the masticatory cycle which were not directly orthal; in primitive therian mammals the power stroke had a marked transverse component (Crompton & Hiiemäe 1969a & b), while in traversodontids it had a strong posterior component. These movements in the horizontal plane permitted several shearing surfaces to be used as the jaws were closed.

In traversodontids but not in the tritylodontids the mandibular symphysis was massive and presumably immobile during life. The left and right lower postcanine teeth were slightly further apart than the corresponding upper postcanines; the opposite is true of primitive mammals. These two characters of traversodontids suggest that during the final stages of mastication both mandibular rami were drawn directly backwards and occlusion had to occur on both sides simultaneously; the greater the extent of the backward movement the more nearly parallel the rows of postcanine teeth. This is not possible in a primitive mammal (Crompton & Hiiemäe, 1969a & b). Significant transverse mandibular movements in cynodonts and tritylodontids were prevented by the massive transverse processes of the pterygoid

bones and the structure of the postcanine teeth. The structure of the lower jaw of primitive mammals (Crompton 1963, Krebs 1969) suggests that remnants of the transverse processes of the pterygoids may have been present in some cases; it is possible that their reduction in early mammals was coupled with changes in jaw musculature permitting the introduction and strengthening of transverse mandibular movements.

The mechanism involved in developing occlusion in gomphodont cynodonts and in mammals (Crompton & Jenkins, 1968) appear to have been similar. In the early forms of both groups the crowns of corresponding upper and lower teeth were shaped by wear to produce matching shearing planes; in both a complex series of cusps and ridges had to be obliterated by wear before the teeth could function efficiently. This is particularly true of the cynodont *Diademodon*, of the new species of *Massetognathus* and of the mammal *Eozostrodon* (= *Morganucodon*). In the later traversodontids, tritylodontids and mammals the postcanines and molars lacked superfluous crown structures that had to be worn down and the crowns already possessed shearing planes that were genetically determined rather than produced by wear. The numerous Middle Triassic cynodonts from South America and the abundant early mammal teeth should be studied in detail in order to clarify further this aspect of evolutionary change.

The distribution of traversodontid cynodonts is briefly discussed; it suggests ready access between the continental masses of Africa and of South America during the Trias. The Traversodontidae may nevertheless have had a worldwide distribution.

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## ABBREVIATIONS USED IN TEXT-FIGURES

a.a.c.l.	anterior accessory cusp of lower postcanine	i.c.l.	internal cusp of lower postcanine
a.a.c.u.	anterior accessory cusp of upper postcanine	i.c.u.	internal cusp of upper postcanine
a.r.	anterior ridge	p.a.c.	posterior accessory cusp
a.v.	anterior valley	p.b.	posterior basin
a.w.	anterior wall	p.c.	posterior cingulum
b.l.	basin in lower postcanine	p.r.	posterior ridge
b.u.	basin in upper postcanine	p.v.	posterior valley
c.c.u.	central cusp of upper postcanine	p.w.f.	postcanine wear facet
e.	embayment	s.	saddle
e.cing.	external cingulum	Sh.s.	shearing surface
e.c.l.	external cusp of lower postcanine	t.r.	transverse ridge
e.c.u.	external cusp of upper postcanine	t.r.l.	transverse ridge of lower postcanine
en.	enamel	t.r.u.	transverse ridge of upper postcanine
		w.f.	wear facet.

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